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Plants from Turkey Introduced with Manganese Ore into a Place in Västergötland (Sweden)

By GUNNAR DEGELIUS

Botanic Garden, Göteborg

Alien plants often enter an area by the unintentional aid of man. Various kinds of human activity may be of importance, but, nowadays, the factory industry is especially important in this connection. The imported raw material (of different kinds and from different countries) often contains diaspores of various plants. Before the working up, this raw material will sometimes be stored near the factory buildings, and the waste products dumped there after the working up. Very often the latter products will be dumped in common dumping grounds outside the communities (where also other waste products are to be found). (However, now the waste products are often burnt, a procedure which influences the recruiting of the alien flora.) This foreign flora is usually not very rich in species (nor in individuals) in one and the same place, but sometimes one may find a surprising accumulation of interesting plants. Concerning rich dumping-grounds in or near Swedish towns, see, e.g., "Stockholmstraktens växter", Qvarfort 1927, Witte 1904, Ahlner 1929, Fries 1945, Sandberg & Westfeldt 1939, Snell 1929, Blom 1933, Tufvesson 1933; further, papers cited in these works, especially those by Blom. Of special interest are such places where a certain kind of raw material has been stored or dumped, thus, where all the alien plants have been introduced in the same way and often from the same area (which may somewhat facilitate the determination of the plants). The very rich flora introduced with wool in some places (e.g., in Lackalänga in Skåne, see Blom 1930, Lange, Flinck & Hylmö 1954, and other literature cited there) may be mentioned in this connection, further that introduced with cork (e.g., near Helsingfors in Finland, see Pettersson 1941, 1952; near Sorö in Denmark, see Wiinstedt 1954), and that with Japanese soya beans

for oil-manufacture (e.g., at Kalmar, see Snell l.c.). The mill industry has also been of great importance for the alien flora (see, e.g., Laurent 1920, Hanssen & Nordhagen 1930, Tambs Lyche 1931, 1934, 1938). At Kvam in Hordaland, Norway, many alien plants have been found on stacks of chromium ore from Asia Minor (Lid 1952, 1955), and at Domnarvret in Dalarne, Sweden, several plants on manganese ore from Russia (Almquist 1949 p. 69). A very rich and interesting alien flora will be treated below, introduced with manganese ore from Turkey to Vargöns Bruk, paper mill and smeltery, in Västra Tunhem parish in Västergötland, S.W. Sweden. This ore comes, more exactly, from the seaport town of Silivri on the northern shore of the Sea of Marmara, i.e., from the European part of Turkey, province of Istanbul. (The mines are said to be situated above the harbour in S.)

The alien flora at Vargön was for the first time observed — in the beginning of August 1958 — by Mr. Bertil Hansson, manager buyer of the factory, who informed the Botanic Garden in Göteborg of the case. Twice — 21/8 and 29/9 — I visited the locality, together with Mr. Hansson. For closer investigations I collected material of all the plants. (Stacks of manganese ore from other parts of the world — Russia, India, West and South Africa — were also studied by me, but, as these stacks were older, an eventually earlier occurring alien flora had now disappeared.)

The manganese ore from Turkey was divided into three separate stacks, placed closely beside each other, in open places just south of the smeltery office within the factory grounds. They covered together an area of approximately 600 m². The ore has been here since November 1957 (the two stacks most rich in plants) and April 1958 (the third stack). It occurred in loose clods, and only the upper side of the stacks was more strongly compressed (owing to the pressure of the tipping trucks). The ore was quite naked, nowhere covered by earth. The working up of the ore began at the end of 1958, and during the year 1959 the stacks will evidently disappear.

This manganese ore is mineralogically a psilomelane (MnO₂) of sedimentary origin. The percentage of Mn is 37—40 %. Further there are, inter alia, 3—4 % Fe, 13—15 % SiO₂, 0.2 % P, 15 % CaCO₃ (communication from the factory). The ore is porous and watery.

The flora and vegetation was most abundantly developed on the plane and hard parts of the stacks, especially those from 1957 (cf. above), but nowhere was the vegetation quite close (the plants were spread or here and there somewhat heaped). On the more loosely built steep sides, the

vegetation was much more sparse. In spite of the poor soil, many species were particularly luxuriant (cf. below), evidently because the past summer was rich in rain (especially July in these parts of the country; the summer was not very warm, but the autumn unusually mild).

28 families are represented in the following list, the predominant of which are *Gramineae* (17 species), *Leguminosae* (16), and *Compositae* (15).

The total number of species is 119, at least 94 of which must have been introduced with the ore since they do not belong to the wild or subspontaneous flora in the neighbourhood (however, several of the remaining 25 species have probably also been introduced). Most plants are annual, the exceptions being only 6.7 % (for the main part perennial). Especially abundant were: *Setaria viridis*, *Urtica urens*, *Chenopodium vulvaria*, *Amaranthus albus*, *A. blitoides*, *Fumaria officinalis*, *Coronopus squamatus*, *Anagallis femina*, *Chaenorrhinum minus*, *Galium tricornis*, and *Senecio viscosus* (last-mentioned plant locally on one of the stacks). Among the more sparsely occurring species, many belong to the rare alien plants in Sweden. The following five have never been found in our country previously: *Nigella arvensis*, *Trifolium leucanthum*, *Thymelaea passerina* (also the genus is new), *Bupleurum Heldreichii*, and *Legousia pentagonia*.

Particularly luxuriant and conspicuous were (some, however, occurring sparsely): *Polygonum kitaibelianum*, *Atriplex tatarica*, *Amaranthus blitoides*, *Gypsophila porrigens*, *Rapistrum rugosum*, *Malva nicaeensis*, *Kickxia spuria*. Some other species appeared in small specimens only, a few as pure dwarfs (e.g., *Bupleurum lancifolium*, *B. Fontanesii*, *Scorpiurus sulcatus*, *Anthemis altissima*). Most species came in flower and fruits; in the last case several also had ripe seeds (among the undoubtedly alien species at least: *Polygonum kitaibelianum*, *Chenopodium vulvaria*, *Amaranthus albus*, *A. blitoides*, *Vaccaria pyramidata*, *Gypsophila porrigens*, *Sisymbrium irio*, *S. polyceratium*, *Melilotus indicus*). Quite sterile were: some *Chenopodium* spp. (see the list), *Atriplex tatarica*, *Sanguisorba minor* (coll.), *Stachys* sp., *Solanum lycopersicum*, the *Xanthium* spp., *Helianthus annuus*, and *Tussilago*.

Introduced floras of this type (cf. above) are usually short-lived, due to different causes, even if some species remain and perhaps also spread to the surroundings (despite the strong competition with the more or less indigenous flora). The Turkish flora treated here, at least the main part of the species, is doomed to disappear already this year — i.e., after

one or perhaps two vegetation periods — because of the quick working up of the ore (cf. above).

All the species found at Vargön belong to the flora of the Mediterranean area, even though many of them have originally been introduced there. Some are widely distributed in the area mentioned. On the Balcan Peninsula, about half of the species grow *in ruderalis* and similar places (according to Hayek's flora), thus, they do not belong to the true native vegetation.

The east part of the old province of Thrace (belonging to European Turkey), from which the plants mentioned here derive, is, like the adjacent part of Asiatic Turkey (Bithynia), by no means unknown as to the phanerogamous flora. Several papers by various authors have treated this flora (see, e.g., Rechinger fil. 1938 and Czegezott 1939 pp. 129—135 as well as literature cited there). Most species at Vargön are mentioned in these papers. A special work on the plant geographical position of Eastern Thrace has been published by Mattfeld (1929). According to the map there, the town of Silivri belongs to the narrow Mediterranean region of the province in question.

The plants collected have been identified by the aid of the floras of Hayek, Halácsy, Boissier, and others, but several special works on various genera have also been studied. The determination work has been highly facilitated by the very rich material of Mediterranean plants (the former Herb. Hayek especially) in the herbarium of Göteborg, as well as of alien plants in the Scandinavian collection there, the latter revised and to a large degree also collected by Dr. Carl Blom, our foremost expert in the alien flora of Scandinavia. Dr. Blom has kindly identified two of the species from Vargön, and my own determinations have been checked by him in some cases (mentioned in the list). Mr. Ian C. Hedge and Mr. I. Roberts (Edinburgh) have kindly determined two specimens. — The plants are kept in the herbarium of the Botanic Garden of Göteborg; duplicates have been delivered to the herbaria of Stockholm (Riksmuseet) and Oslo.

List of Species

All the plants found on the manganese ore are mentioned below, thus, also those species which perhaps have spread to the stacks from the surroundings (a minority, cf. above). Unless otherwise stated, the plants are fertile (with buds, flowers, or fruits; for numerous species, especially alien ones, closer information is given). — The nomenclature is, in applicable parts, in agreement in the main with Hylander 1955, also the arrangement.

Gramineae

- Setaria viridis* (L.) P.B. — Rather common. The normal low type (culms usually 8—20 cm, some lower) with small panicles.
- S. verticillata* (L.) P.B. — A few specimens. The normal type with backward-pointing teeth of bristles.
- Lolium perenne* L. — Some specimens.
- L. temulentum* L. — A few specimens. The normal type with coarse awns.
- Avena sativa* L. — Some specimens.
- Alopecurus myosuroides* Huds. — A single rather large specimen with several panicles.
- Phleum subulatum* (Savi) A. & G. — Some small specimens. Det. C. Blom.
- Phalaris paradoxa* L. — Some small specimens. Belong to var. *praemorsa* Coss. & Dur.
- Bromus madritensis* L. — Some specimens.
- B. arvensis* L. — Many specimens.
- B. japonicus* Thunb. — A single small specimen.
- Brachypodium distachyum* (L.) P.B. — A single specimen. Belongs to f. *multiflorum* Willk.
- Triticum monococcum* L. — A single specimen.
- Aegilops speltoides* Tausch — Some specimens. Belong to var. *ligustica* (Bert.) A. & G.
- Ae. triuncialis* L. — Some specimens.
- Hordeum vulgare* L., em. Lam. — Some specimens.
- H. murinum* L. — Some specimens. Belong to subsp. *leporinum* (Link) A. & G. (confirm. C. Blom).

Urticaceae

- Urtica urens* L. — Rather common.
- U. pilulifera* L. — A single small specimen.

Polygonaceae

- Polygonum heterophyllum* Lindm. — Several large specimens (up to nearly 2 m wide).
- P. kitaibelianum* Sadl. — Several large specimens (up to about 1.5 m wide), many-branched. One of the most conspicuous plants here. Owing to the rather large fruits (2.5 mm long), this plant must be referred to the species mentioned, not to the related *P. patulum* M.B. With ripe seeds.
- P. convolvulus* L. — Some specimens.

Chenopodiaceae

- Chenopodium album* L. — A single about 1 m high specimen, many-branched, sterile. Belongs to var. *Borbasii* (J. Murr.) A. Ludw. (confirm. C. Blom).
- Ch. opulifolium* Schrad. — Some sterile specimens.
- Ch. ficifolium* Sm. — A single sterile specimen.
- Ch. vulvaria* L. — Rather common. With ripe seeds.
- Ch. urbicum* L. — A single rather small specimen.
- Atriplex patula* L. — A single rather large specimen. A type with narrow leaves.
- A. tatarica* L. — Some large sterile specimens.

Amaranthaceae

- Amaranthus retroflexus* L. — Some specimens, only one fertile (confirm. C. Blom).
A. albus L. — Rather common. With ripe seeds.
A. blitoides S. Wats. — Common, perhaps the most common plant here. Some specimens very large and luxuriant. With ripe seeds.
A. deflexus L. — A single small specimen.

Caryophyllaceae

- Spergula salina* (J. & C. Presl) D. Dietr. — A single large specimen. The normal type with leafy inflorescences.
Herniaria glabra L. — A few small specimens. The type with short-haired stems and glabrous leaves. Evidently introduced here (it is rare in Västergötland).
H. hirsuta L. — Some \pm small specimens.
Melandrium noctiflorum (L.) Fr. — A single specimen.
Vaccaria pyramidata Med. — Some small or rather large specimens. Ripe seeds. It belongs to var. *grandiflora* (Fisch.) Hayek.
Gypsophila porrigens (L.) Boiss. — Two very large specimens (the largest one about 1.5 m wide). Ripe seeds. — An aberrant type: more glandular than usually, also the sepals strongly glandular. Other specimens introduced to Sweden, which I have seen (from Göteborg), belong to the normal type.

Ranunculaceae

- Nigella arvensis* L. — A single small specimen (in flower). — This annual herb is new to the alien flora of Sweden (but it is found in Denmark: near Horsens, see Lange 1872 p. 306, 1896 p. 273). Total distr.: Central Europe, Mediterranean area. On the Balcan Peninsula, it occurs "in agris, collibus apricis" (Hayek's flora). A rather polymorphic species (see Boissier's flora I p. 66; however, cf. Bornmüller 1936 p. 12); my plant is too young and small for a closer determination as to type.

Papaveraceae

- Glaucium flavum* Cr. — A fertile specimen (in bud) and some sterile rosettes. Ovary \pm glabrous.
Papaver rhoeas L. — Some rather small specimens.
Fumaria officinalis L. — Rather common. A somewhat broad-leaved type.
Hypecoum pendulum L. — A single small specimen (in flower and fruit, fruits not quite ripe). — According to "Stockholmstraktens växter" (ed. 1 and 2), collected in Stockholm: Sabbatsberg (1889 J. W. Hamner); samples not found in our great herbaria. Evidently a very rare plant in Sweden.

Cruciferae

- Sinapis arvensis* L. — Some specimens (in flower and fruit). Belong to var. *schkuhriana* (Rehb.) Hagenb. f. *hirsuta* Beck. Evidently introduced.
Rapistrum rugosum (L.) All. — At least one specimen, large and many-branched (in flower and fruit). Belongs to subsp. *orientale* (L.) R. & F., and the type with glabrous fruits.

- Lepidium campestre* (L.) R.Br. — A single specimen (in flower and fruit).
Coronopus squamatus (Forsk.) Asch. (syn. *C. procumbens* Gilib.). — Rather common. In part large and well-developed specimens (also richly fruiting).
Capsella bursa-pastoris (L.) Med. — Some specimens. Fruits typical.
Sisymbrium irio L. — A single specimen, many-branched. Ripe seeds.
S. officinale (L.) Scop. — At least some specimens.
S. polyceratium L. — Many specimens, \pm large and well-developed (richly fruiting, in part ripe seeds). Belong to the normal type with glabrous stem, well-developed bracts, etc. — Other samples from Sweden, which I have seen (from Göteborg, leg. Blom, and Gävle, leg. Ahlner), are very small compared with those from Vargön.
Descurainia sophia (L.) Prantl — At least some specimens.

Rosaceae

- Sanguisorba minor* Scop. (coll.). — A few sterile rosettes.

Leguminosae

- Ononis repens* L. — A single rather small specimen (in flower).
Trigonella monspeliaca L. — Some small or rather large specimens (in flower, also abundantly fruiting). Belong to "var. *typica* Eig", according to the key in Feinbrun 1933 (p. 392).
Medicago lupulina L. — Several specimens (in flower and fruit). Belong to var. *glandulosa* Mertens & Koch.
M. hispida Gaertn. — Some specimens (in flower and fruit). Belong to var. *hispida* [syn. var. *denticulata* (Willd.) Urb.].
Melilotus albus Desr. — Several specimens.
M. officinalis Lam., em. Thuill. [syn. *M. petitpierranus* (Hayne) Willd.]. — Several large specimens (in flower and fruit).
M. indicus All. — Several specimens (in flower and fruit, in part ripe seeds).
Trifolium resupinatum L. — A single small specimen (in flower).
T. leucanthum M.B. — A single specimen (in flower). Belongs to the main type (with whitish flowers) and its f. *appressopilosum* Thell. — This annual herb is new to the alien flora of Sweden. Total distr.: Mediterranean area, Hither Asia; further introduced in some places in Central and South Europe. On the Balcan Peninsula, it grows "in rupestribus dit. medit." (Hayek's flora). — A related species is *T. echinatum* M.B., also (rarely) found in Sweden. It differs from the first-mentioned plant in some characteristics, most important of which seems to me to be in the teeth of the sepals. These are in *T. echinatum* of unequal length and breadth, in *T. leucanthum* they are equal or subequal.
T. lappaceum L. — A single rather large specimen (in flower). Belongs to the main type (acc. to Hayek's flora).
Coronilla scorpioides (L.) Koch — A few specimens (in flower and fruit).
Scorpiurus sulcatus L. — A single specimen of dwarfy size (in flower, one young fruit). — This species was found for the first time in Sweden as late as in 1949 (at Gävle, see Levan 1950 p. 473).
Vicia sativa L. — Some specimens (in fruit). A type with narrow leaves (f. *linearis* Lge).

V. peregrina L. — Some specimens (in flower and with \pm ripe fruits).

V. bithynica L. — A single small specimen (\pm in flower).

Lathyrus aphaca L. — A few specimens (in flower and fruit, some fruits \pm ripe). Belong to the main type (with solitary flowers).

Geraniaceae

Erodium chium (L.) Willd. — A single large specimen (in flower). — Found twice in Sweden previously: at Gävle 1921 (Ahlner 1929) and Göteborg, Ringön, 1955 Carl Blom (Herb. Gotob., a single small specimen in flower).

Zygophyllaceae

Tribulus terrestris L. — Some small specimens (without fruits).

Euphorbiaceae

Euphorbia exigua L. — A single small specimen.

E. falcata L. — As the preceding species (also fruits).

Mercurialis annua L. — Several specimens (σ and φ).

Malvaceae

Malva silvestris L. — Some specimens (in flower, \pm young fruits). A type with strongly hairy fruits (acc. to Hayek's flora: var. *incanescens* Griseb. f. *eriocarpa* Boiss.).

M. nicaeensis All. — Some large specimens (in flower, \pm young fruits).

Cucurbitaceae

Ecballium elaterium (L.) Rich. — Some rather small specimens (partly in flower).

Thymelaeaceae

Thymelaea passerina (L.) Coss. & Germ. [syn. *Lygia passerina* (L.) Fasano, *Passerina annua* Wikstr.]. — A single small specimen (in flower). Belongs to the glabrous main type. — This annual herb is new to the alien flora of Sweden. Total distr.: Central, South and East Europe, West Asia. On the Balcan Peninsula, it grows "in lapidosis, cultis" (Hayek's flora).

Umbelliferae

Scandix pecten-veneris L. — Some specimens (in fruit).

Torilis nodosa (L.) Gaertn. — Two small specimens (in fruit).

Caucalis lappula (Web.) Grande — A single specimen (in fruit). Belongs to var. *lappula*. [The other race, var. *muricata* (Gr. & G.) Hyl., with stunted spines, is much rarer in Sweden.]

Bifora radians M.B. — Two rather small specimens (in fruit).

Conium maculatum L. — Some rather large specimens (in flower and fruit).

Bupleurum lancifolium Hornem. (syn. *B. protractum* Hoffmannsegg & Link). — A single dwarfy specimen (in flower, young fruits).

B. Heldreichii Boiss. & Balansa — A small specimen (in fruit). Det. I. Roberts.
— This annual herb is new to the alien flora of Sweden. It was described in Boissier 1859 (p. 75), from Asia Minor ("in arvis" in Pisidia, and "in agris arenosis" in Cappadocia). It is closely related to the preceding species, but differs in having more rounded upper leaves, narrower fruits, and — first and foremost — much narrower bracteoles.

B. Fontanesii Guss. — As *B. lancifolium*.

Primulaceae

Anagallis arvensis L. — A single specimen (in flower).

A. femina Mill. — Rather common. In flower and fruit. Petals blue, marginally toothed, \pm without glandular hairs. (Cf. Hylander 1945 p. 256.)

Heliotropiaceae

Heliotropium europaeum L. — Several specimens. A type with large flowers (5 mm broad); similar plants collected in Sweden previously (specimens in Herb. Gotob.).

Boraginaceae

Lithospermum arvense L. — A single small specimen.

Myosotis arvensis (L.) Hill — At least one specimen.

Labiatae

Galeopsis tetrahit L. — As the preceding species.

Stachys sp. — Some sterile rosettes (*lanata*-type).

Solanaceae

Hyoscyamus niger L. — Some specimens.

Solanum lycopersicum L. — Some young sterile plants.

S. sp. — A single small specimen (in flower). In some characteristics similar to *S. alatum* Moench, but probably not belonging to that species.

Scrophulariaceae

Kickxia elatine (L.) Dum. — Several specimens (in flower and fruit). Belong to the common type (with glabrous pedicels).

K. spuria (L.) Dum. — Many specimens (in flower). Besides normal plants, two aberrant types occurred. One of the latter (most common type of the species here) has whitish lower lip on the fully developed flowers (instead of yellow) and violet spur (not pale); the plants are often very large (up to 85 cm long), decumbent, many-branched. The other aberrant type — a single specimen — is less hairy (according to Mr. Hedge, who has examined the plant, it must be referred here).

Chaenorrhinum minus (L.) Lge — Common (as in the surroundings).

Scrophularia canina L. — A single large and many-branched specimen, nearly sterile (only a few flowers). — This species seems to have been collected only once in Sweden previously (in Stockholm 1882, see Cedergren 1919 p. 487, 1922 p. 15).



Fig. 1. *Legousia pentagonia*, the specimen from Vargön.

Plantaginaceae

Plantago indica L. — A single large and many-branched specimen (in flower).

Rubiaceae

Galium tricornis Stokes — Rather common, but small specimens (in fruit).

Campanulaceae

Legousia pentagonia (L.) Thell. [syn. *Specularia pentagonia* (L.) DC.]. — A single specimen (in flower). A glabrous type. Fig. 1. — This annual herb is new to the alien flora of Sweden. Total distr.: eastern Mediterranean area; introduced in some places in Central and South Europe (see Thellung 1912 p. 495, Hegi's flora VI: 1 p. 366). According to Krause (1928 p. 93),

it is common ("häufige Ruderalpflanze") all over Asia Minor. On the Balcan Peninsula, it occurs "in cultis, agris dit. mediet." (Hayek's flora). From *L. speculum-veneris* (L.) Schinz & Thell., also found in Sweden, it differs, inter alia, in larger corolla (usually 1.5—1.8 cm long, in the other species 1—1.2 cm) as well as in longer ovaries (in my specimen usually about 2.5 cm long) and fruits.

Compositae

Xanthium strumarium L. — A single young and sterile specimen.

X. spinosum L. — Some \pm small and sterile specimens.

Helianthus annuus L. — Some young and sterile specimens.

Anthemis austriaca Jacq. — A single specimen.

A. altissima L. (syn. *A. cota* L.). — A single dwarf specimen.

A. arvensis L. — Several specimens.

A. ruthenica M.B. — A single specimen. Det. C. Blom.

A. cotula L. — Some specimens.

Matricaria inodora L. — Some specimens.

M. recutita L. (syn. *M. chamomilla* L.). — Several specimens.

Tussilago farfara L. — Some rosettes of leaves.

Senecio viscosus L. — Abundant on one of the stacks.

Centaurea calcitrapa L. — A single rather large specimen (with young heads).

C. solstitialis L. — Some specimens (with \pm young heads).

Picris echioides L. — A single specimen (in flower).

Göteborg (Gothenburg), Botanic Garden, in March 1959.

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Bestandesaufnahme der Ackerunkrautvegetation in einigen westschonischen Gemeinden 1958

Von H. MERKER

Meddelanden från Lunds Botaniska Museum Nr 133

(Med en sammanfattning på svenska)

Im Frühjahr und Sommer 1958 wurde eine Erfassung der Ackerunkrautvegetation in 16 Gemeinden Westschonens, von der Küste bis ungefähr 15 km gegen das Landesinnere durchgeführt (Fig. 1). Sie erstreckte sich über die Monate Mai bis einschliesslich August. Es wurden nur jene landwirtschaftlichen Flächen berücksichtigt, die an alljährlichem oder wenigjährigem Fruchtwechsel teilnehmen; Dauergrünland wurde nicht erfasst. Feldmässiger Gemüsebau wurde einbezogen, dagegen nicht Gartenland und Ruderatflächen. Wo noch Brachen vorkommen, was vor allem in den Sandgebieten der Fall ist, haben sie sich durchwegs als ergiebige agrarbotanische Objekte erwiesen. Da gerade diesen Flächen eine nicht geringe Bedeutung als Unkrautsamen-Produktionszentren zukommt, von denen aus nähere und weitere Anbaugebiete ihre floristischen Bestände auffüllen können, erschien es notwendig, auch diese Type von Ackerland einzubeziehen. Dies erklärt, dass einige ausgesprochene Wildpflanzenarten im Verzeichnis auftreten.

In sämtlichen Fällen wurde eine vom Rande wenigstens 5 Meter entfernte, durchschnittlich 100 m² umfassende Fläche inventiert. Vereinzelt wurde auch die Randflora notiert, wenn dies zweckmässig erschien. Die Form der Fläche war nicht immer gleich, meist quadratisch oder streifenförmig. Arten, die in ihren Jugend- und Erstarkungsstadien nicht unmittelbar bestimmt werden konnten, wurden später an Ort und Stelle im floralen Zustand ermittelt oder im Garten bis zum Eintritt des Blühens und Fruchtens kultiviert. Von ungewöhnlichen wie auch unsicheren Arten wurden Proben gepresst und fallweise Samen geerntet. Für die Bestimmung der Arten im postembryonalen und jugendlichen

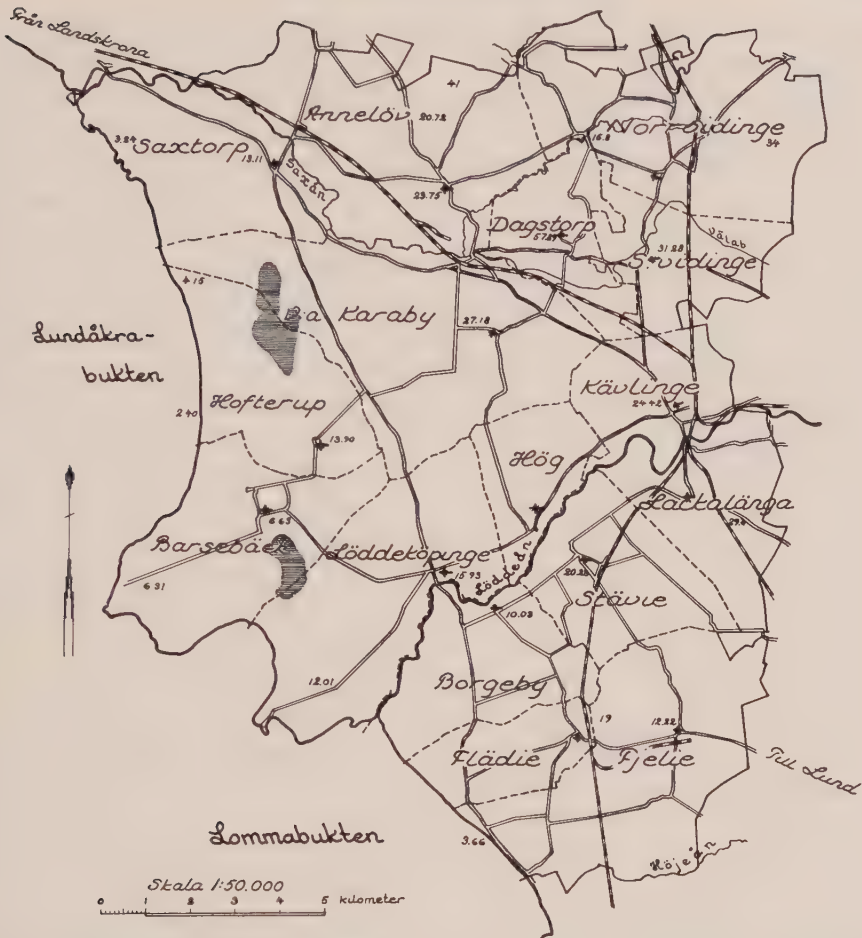


Fig. 1. Das Untersuchungsgebiet umfasst 16 Gemeinden von der Küste bis etwa 15 km gegen das Landesinnere im Raume zwischen Lund—Landskrona und enthält ein Netz von 300 Arbeitsflächen.

Entwicklungszustande war das Werk N. Sylvén's „Om de svenska dikotyledonernas första förstärkningsstadium“ (10) eine hoch einzuschätzende Hilfe.

Von den netzförmig über das etwa 200 km² umfassende, flache bis schwach hügelige Gebiet ausgelegten 300 Erhebungspunkten wurden Bodenproben entnommen. Die Bodenart wurde zunächst im Gelände bestimmt und soll späterhin im Laboratorium weiter untersucht werden. Der Säuregrad der Proben wurde unmittelbar im Laboratorium gemessen. Die Bodenverhältnisse im berührten Gebiet sind uneinheitlich, so

gut wie alle Stufen zwischen Sand- und Tonböden, wie auch pH-Werten zwischen 4,9 und 8,5 (Aug.) sind vertreten. Genetisch sind sie hauptsächlich Moränen, glazifluviale, marine, fluviale und moorige Bildungen (9). Die vorteilhaftesten Bonitäten liegen, im Durchschnitt gesehen, auf Moränenlehmen. Parallel damit weist auch die Struktur der Höfe gewisse Verschiedenheiten auf, es muss aber hervorgehoben werden, dass der weitaus grösste Teil intensivst bewirtschaftet wird. Es sei besonders auf den reichlichen Hackfruchtbau und auf die allgemein übliche kemische Unkrautbekämpfung im Getreide durch Frühljahrs-spritzung hingewiesen. Topographisch ist das Gebiet vorwiegend Ebene, die höchstbelegenen Arbeitsflächen erreichten nicht 50 m S.h., der höchste Punkt, 69 m S.h., liegt in einer etwa 4 km langen Hügellandschaft im nördlichen Teil.

Die Temperaturen hielten sich im Untersuchungsjahr auch noch im Mai unter den Normalzahlen, die Niederschläge dagegen über den normalen, sodass das Frühjahr als ausgesprochen spät und nass zu bezeichnen ist. Das ermöglichte es, zunächst die überwinterte Unkrautvegetation zu erfassen, ohne dass sich noch die Keim- und Erstarkungsstadien der Frühljahrsannuellen in das Bild drängten.

Winterungen wurden nach Möglichkeit zweimal begangen: das erste Mal im Mai—Juni, um die ausdauernd und postembryonal überwinterten Arten zu erfassen, das zweite Mal im Juli—August, um den Sommerzustand kennen zu lernen. Sommerungen wurden von Mitte Juni an in der Regel nur einmal besucht.

Um die Aufnahmepunkte rasch und genau wiederfinden zu können, wurden über den die Örtlichkeit beschreibenden Erhebungskopf im Feldbuch hinaus auf zwei an der Landkarte befestigten Transparentpapieren (Oleaten) die jeweils deckenden Buchführungsnummern der ersten und zweiten Erhebung über dem Zirkelstich der Landkarte eingetragen.

Wegen der im kalten und nassen Frühjahr späten Bestellung der Sommerungen, wie auch wegen der dann noch verzögerten Vegetation waren diese Schläge auf Wochen hin unkrautfrei. Andererseits wurde auch die Pflege der Winterungen dadurch erschwert, dass rechtzeitiges Hacken verhindert wurde und gehacktes Unkraut dann noch in grossem Umfange sich rasch wieder regenerieren konnte. Die Unkrautflora hatte deshalb z.B. im Raps eine verhältnismässig günstige Ausgangslage.

Die Entwicklung der sommerannuellen Unkrautvegetation wurde durch eine mehrwöchige Hitzewelle von Mittsommer bis nahezu Mitte

Juli beeinträchtigt, sodass auf leichteren Böden die Jugendstadien der Unkrautbestände wegtrockneten oder mehr oder weniger nur ein Kümmererstadium erreichten. Dies trifft in besonderem Masse für die Winterungen und Frühjahrssaaten zu und lässt die Frequenz mancher sommerannueller Arten, verglichen mit Verhältnissen anderer Jahre, vermutlich niedriger erscheinen, was wohl teilweise auch für Hackfrüchte gelten mag. Nach Aussage einer hiesigen Spritzdienstfirma soll der Unkrautbekämpfungseffekt sehr zufriedenstellend gewesen sein.

Die angeführten Verhältnisse lassen es für die Gliederung der vorliegenden Mitteilungen zweckmässig erscheinen, über einen **Frühjahrs- und Sommeraspekt** zu berichten.

Soweit die aus dem Feldbuch zitierten oder in der Tabelle enthaltenen Aufstellungen Bestandsdichtezahlen anführen, liegt das Verfahren und die Skala nach Braun-Blanquet zu Grunde, (3) und (11). Dem nach bedeutet

5,	dass die Art mehr als	75 %	der Fläche deckt			
4	„ „ „ „ „	50—75 %	„ „ „			
3	„ „ „ „ „	25—50 %	„ „ „			
2	„ „ „ „ „	5—25 %	„ „ „			
1	„ „ „ „	weniger als 5 %	„ „ „			
+	„ „ „ „	spärlich vertreten ist				
r	„ „ „ „	selten ist				

Ein Dekungsgrad mit erhöhtem Ring, z.B. $+^{\circ}$ bedeutet, dass die Art kümmerst, erhöhter Punkt dagegen, dass die Art üppig entwickelt ist, z.B. 3'.

Um das umfangreiche Material einigermaßen vergleichbar wiederzugeben, wurde eine tabellarische Übersicht zusammengestellt. Sie enthält für jede Gemeinde und Pflanzenart links in den Spalten die Anzahl Vorkommen, rechts den vorherrschenden (häufigsten) Deckungsgrad, ausserdem eine Spalte Frequenzzahlen, bezogen auf das ganze untersuchte Gebiet. Sie wurden so errechnet, dass die Summe eines Artvorkommens aller Gemeinden durch die Summe der Erhebungen sämtlicher Gemeinden gebrochen wurden.

Die hier verwendete Nomenklatur geht nach Nils Hylander's Verzeichnis über die Pflanzen des Nordens, 1955 (5). Komplizierte Gruppen wurden bis auf weiteres kollektiv behandelt.

Frühjahrsaspekt

Es haben sich deutliche Unterschiede schon in der Artenzusammensetzung und dem Grad der Erstarkung der überwinterten Streckungs- und Jungpflanzenstadien der Unkrautvegetation in den verschiedenen



Fig. 2, 3. Durchschnittpflanzen von *Triplespernum maritimum* var. *insidiosum* (= *Matricaria inodora*), Stettin und *Papaver rhoeas* aus verschiedenen, jedoch unvollständigen Folienfrüchten. Der Standort der grossen Pflanzen war Raps, der der kleinen Beizen. Die Blüten sind als gleich zu bezeichnen, die Pflanzen wurden am gleichen Tage, 21.5.1948, entnommen.



Fig. 5. Vor allem auf den Lichtfaktor zurückzuführende, unterschiedliche Durchschnittsentwicklung von *Arenaria serpyllifolia* in Raps. Links aus normalem Reihenbestand mit Deckungsgrad 4, rechts aus schütter bestandenem Angewende mit D.gr. 1—2. Zeitpunkt: 17.6.1958.

Kulturen und auf ungleichartigen Böden ergeben. Eine bestimmte Art scheint sich am selben Ort, jedoch in unterschiedlichen Kulturen, anders entwickeln zu können. Der Unterschied war innerhalb der Cerealien nicht so stark zwischen Unkräutern des Weizens und Roggens, auffällig jedoch zwischen Getreideunkräutern und Rapsunkräutern (Fig. 2—5). Die letzteren waren meist grossblättrig, grossrosettig, langtriebig und mastig, sie machten den Eindruck von Gigasformen. Der Grund für dieses Erscheinungsbild dürfte wohl vor allem darin zu suchen sein, dass der Raps im Gegensatz zu den Getreiden überlegene Stickstoffdüngung erhält.

Raps

Die Deckungsgrade für Unkräuter im Raps fielen, verglichen mit denen der Getreide, im Durchschnitt höher aus, ohne dass dies eine höhere Individuenzahl zu bedeuten braucht. Eine üppige *Stellaria media*-Pflanze z.B. deckt nun einmal mehr Boden als eine magere. Die Bedeutung dieser Begünstigung der Unkrautflora für das Auffüllen der Samen-

reserven im Boden erschien offenbar. Im Raps sind die Arten jedoch nicht mit dem Zeichen für besondere Begünstigung versehen, nur Einzelfälle bilden eine Ausnahme. Ein wahllos aus dem Feldbuch herausgegriffenes Beispiel für Raps sei hier angeführt.

14/2 Kopf mit Örtlichkeit (nahe Lund) Raps D.gr. 2/3.

Boden: dunkelgraubrauner lehmiger Sand von loser Struktur, pH 6,8, eben.

Datum: 10.5.1958.

Menge	Art	Entwicklungszustand
1	<i>Veronica persica</i>	überwintert, blühend
2	<i>Stellaria media</i>	„ „
+	<i>Viola arvensis</i>	„ „
+	<i>Capsella bursa-pastoris</i>	überwinterte Rosetten
+	<i>Elytrigia repens</i> (<i>Triticum</i>)	Rhizomtriebe
2	<i>Poa annua</i>	junge Büschel, blühend
2	<i>Tripleurospermum maritimum</i> v. <i>inodorum</i> (<i>Matricaria</i>)	beginnende Streckung
+	<i>Centaurea cyanus</i>	„ „
+	<i>Lamium amplexicaule</i>	überwintert, Blütenknospen
+	<i>Myosotis arvensis</i>	Jungpflanzen, überw.
r	<i>Papaver rhoeas</i>	überwinterte Rosetten
r	<i>Galium aparine</i>	„ Jungpflanzen
r	<i>Geranium molle</i>	„ „

Ergänzungen: 14.7.1958.

r	<i>Matricaria matricarioides</i>	blühend-fruchtend
+	<i>Veronica agrestis</i>	„ „

2.8.1958.

r ^o	<i>Chenopodium album</i>	—
+	<i>Polygonum persicaria</i>	—
+	<i>Sinapis arvensis</i>	—

In einer grossen Zahl der Erhebungen in Raps war das fortgeschrittene florale und fertile Stadium und die starke Verbreitung von *Veronica persica* bereits anfang Mai auffällig. Diese Art steht nur unbedeutend *hederifolia* in ihrer Verbreitung nach und übertrifft an Frequenz sowohl *agrestis* als *arvensis*. Für Deutschland wird *Veronica persica* als verbreitet angegeben (8). Als häufig wurden zu Beginn der Vegetationsperiode weiterhin folgende Arten beobachtet: *Anthemis arvensis*, *Apera spica-venti*, *Arenaria serpyllifolia*, *Capsella bursa-pastoris*, *Centaurea cyanus*, *Cerastium holosteoides* und *semidecandrum*, *Cirsium arvense*, *Elytrigia repens* (*Triticum*), *Galium aparine*, *Geranium pusillum*, *Lamium amplexicaule* und *purpureum*, *Tripleurospermum maritimum* v. *inodorum* und stellenweise *Matricaria recutita*, *Myosotis arvensis*, *Papa-*

ver rhoeas, *Rumex crispus* und *Stellaria media*. Auch *Melandrium noctiflorum* trat nicht selten unter den steril überwinternen Arten auf. Das wiederholte Vorkommen von *Saxifraga tridactylites* scheint auch diese Art in die Reihe der bodenständigen (stationären) winterannuellen Ackerunkräuter dieses Gebietes einzuordnen, sie kam nicht nur im Raps, sondern auch in anderen Kulturen überwintert vor.

Roggen

In Uebereinstimmung mit dem Charakter der Roggenböden wurden besonders hohe Artmächtigkeiten bei *Arabidopsis thaliana*, *Arenaria serpyllifolia*, *Cerastium semidecandrum*, *Erophila verna* und *Scleranthus annuus* gefunden, aber auch *Veronica triphylla* trat in überraschenden Mengen auf. Bei ihrem höchsten Deckungsgrad 3 bildete sie fast rasenförmige Gruppen. *Apera spica-venti* ist, im Durchschnitt betrachtet, das führende Roggenunkraut gewesen, fiel aber auch in anderen Feldfrüchten auf. Ob man es 1958 mit einem sogenannten Windhalmjahr zu tun hatte, oder ob diese Artmächtigkeit \pm stetig ist, werden erst Beobachtungen weiterer Jahre entscheiden können. Aus Rücksprachen mit einer hiesigen Unkrautbekämpfungsfirma geht hervor, dass der Windhalm (*Apera*) expandiert. Spritzungen sind wirkungslos, übrigens wird Roggen weniger häufig gespritzt, da er ohnehin weitgehend die meisten Unkräuter niederhalten kann. Bekämpfung mit Kalkstickstoff im Herbst ist noch nicht so populär wie es wohl sein sollte.

Auf den leichtesten Böden waren es die Kleinkreuzblütler *Arabidopsis thaliana* und *Erophila verna* die nebst *Arenaria* die Bodenschicht beherrschten, waren jedoch nur im zeitigen Frühjahr auffallend. Auf diesen Äckern konnte späterhin, offenbar wegen zu grosser Trockenheit, keine Folgevegetation aufkommen, sogar überwinterte *Centaurea* und *Papaver* gelangten dort oft nicht zur Fertilität. Von Interesse dürfte sein, dass nirgends im Gebiet *Agrostemma githago* überwintert beobachtet wurde. Aus den folgenden Ausführungen wird hervorgehen, dass sie auch nicht bei den Sommererhebungen vertreten war. Wehsarg (12) führt an, dass sorgfältige Saatgutreinigung sie gänzlich zum Verschwinden bringt. Dagegen konnten 6 Lokale für *Delphinium consolida* ermittelt werden, die übrigens darauf hindeuten scheinen, dass dieses hier nicht wie in Mitteleuropa kalkhold ist, sondern wohl mehr durch durchlässigen, rasch erwärmbaren Boden bedingt ist. *Delphinium* wurde ausser in Roggen auch auf Brachen gefunden. Die Säuregrade keiner dieser Fundstellen wiesen höhere Werte als 7 auf. Zu erwähnen sei noch, dass

Erodium cicutarium sich gut in Roggen und anderen Winterungen behauptet, es trat aber auch als Sommerkeimer in Massenvegetation auf (in Gurke u.a.).

Winterweizen

Die Begleitvegetation in dieser Kultur wurde hauptsächlich nur in ihren frühesten Stadien erfasst, da die Spritzungen späterhin praktisch nicht viel davon übrigliessen. Man kann sagen, dass die Unkrautvegetation im Winterweizen beim heutigen Stande der Bewirtschaftung hier nur einen kurzfristigen Frühjahrsaspekt hat. Er bestand vor allem aus: *Anthemis arvensis*, *Artemisia vulgaris*, *Centaurea cyanus*, *Cirsium arvense*, *Galium aparine*, *Lamium amplexicaule* und *purpureum*, *Lithospermum arvense*, *Myosotis arvensis*, *Papaver rhoeas*, *Poa annua*, *Tripleurospermum maritimum* v. *inodorum* (*Matricaria*), *Veronica hederifolia*, *persica* und *agrestis*, *Stellaria media*, mancherorts trat *Rumex crispus* hervor, vereinzelt auch *Phragmites communis*, *Polygonum amphibium* und *Tussilago farfara*.

Ein wahllos herausgegriffenes Beispiel:

33/14 Kopf mit Örtlichkeit (nahe Lackalänga), Winterweizen D.gr. 3.

Boden: dunkelgraubrauner mittelschwerer Lehm, pH 7.—, stabile grobklumpige Struktur. Eben.

Datum: 16.5.1958, noch ungespritzt.

Menge	Art	Entwicklungszustand
1	<i>Cirsium arvense</i>	c:a 10 cm Rhizomtriebe
1	<i>Galium aparine</i>	fortgeschrittene Streck.
1	<i>Tripleurospermum maritimum</i> v. <i>inodorum</i>	überwintert
3	<i>Tripleurospermum maritimum</i> v. <i>inodorum</i>	erstes Charakterblatt
r	<i>Myosotis arvensis</i>	überwintert
+	<i>Papaver rhoeas</i>	Rosetten
r	<i>Veronica hederifolia</i>	blüht
2	<i>Polygonum amphibium</i>	austreibende Rhizome
+	<i>Poa annua</i>	blüht
+	<i>Taraxacum vulgare</i>	Rosetten
2	<i>Phragmites communis</i>	austreibende Rhizome
2	<i>Apera spica-venti</i>	Büschelstadium
+	<i>Sinapis arvensis</i>	Keimpflanzen

auf c:a 25 m² ausserhalb der Erhebungsfläche 4—5 *Phragmites communis*.

Futterbau einschliesslich Samenklee

Diese Kulturen gehörten, im Durchschnitt gesehen, zu den weniger unkrautbemengten, sowohl was Artenzahl als auch Individuenzahl be-

trifft. Auf Barstellen leichter Böden wurden grössere Mengen *Senecio vernalis* und *Erodium cicutarium* festgestellt. Soweit Klee, Luzerne und deren Gemische auf ihnen richtig zusagenden Böden lagen, waren sie überwiegend auffällig unkrautarm, sodass oft nicht einmal von Kulturpflanzen völlig unbewachsene Lücken besiedelt waren. Es kam vor, dass Aufnahmen nicht über 4 Arten hinaus kamen, und da noch geringe Deckungsgrade zeigten. z.B. das Kleeraygras 65/32: 1 *Tussilago farfara*, + *Tripleurospermum mar. v. inodorum*, r *Equisetum arvense*, + *Viola arvensis*. In Einzelfällen hatte sich *Erigeron canadense* auf Lücken überwintert und eingenistet. Fertile Bestände von *Tussilago* kamen auch in jüngeren Kleeegrasschlägen vor. Als gering verbreitet ist *Arctium minus* zu bezeichnen. Es kam allerdings nur in sterilen Exemplaren vor. *Apera spica-venti* trat hier stark zurück. *Potentilla anserina* konnte mitunter ins Gewicht fallen, sie war auf etwa 20 Stellen insgesamt anwesend. Im übrigen erschienen je nach den lokalen Verhältnissen grössere Mengen von *Erophila verna*, *Arabidopsis thaliana*, *Arenaria serpyllifolia*, *Cerastium holosteoides* und *semidecandrum*, *Poa annua*, *Galium aparine* u.s.w. Nur stellenweise, z.B. in einigen Samenkleeefeldern, herrschte *Tripleurospermum* vor, man kann jedoch kaum behaupten, dass diese Art das allgemeinste Unkraut gerade des Futterbaus gewesen wäre, sondern seine hohe Frequenz und Artmächtigkeit ist zu einem wesentlichen Teil auch den anderen Kulturen zuzuschreiben.

Um ein artenreicheres Beispiel anzuführen, sei das Gemisch Klee/ital. Raygras 64/31 gewählt:

64/31 Kopf mit Örtlichkeit (Gemeinde Västra Karaby) Klee gras D.gr. 3.
Boden: graubrauner lehmiger sand, pH 6,3. Eben.
Datum: 20.5.1958.

Menge	Art	Entwicklungszustand
r	<i>Veronica agrestis</i>	blüht, fruchtet schwach
r	<i>Tripleurospermum mar. v. inodorum</i>	Streckungsstadium
r	<i>Senecio vernalis</i>	blüht, fruchtet
r	<i>Plantago major</i>	Rosetten
r	<i>Lamium amplexicaule</i>	gering blühend
r ^o	<i>Arenaria serpyllifolia</i>	1/2 cm
+ ^o	<i>Stellaria media</i>	kümmert stark
r	<i>Saxifraga tridactylites</i>	samt, blüht noch
r	<i>Myosotis arvensis</i>	Blütenknospen
r	<i>Papaver rhoeas</i>	Rosetten
r	<i>Equisetum arvense</i>	sterile Triebe
r	<i>Viola arvensis</i>	blüht

Menge	Art	Entwicklungszustand
r	<i>Cerastium holosteoides</i>	grün
+	<i>Cirsium arvense</i>	5—10 cm
r	<i>Lithospermum arvense</i>	Streckungsstadium

Anmerkung: Trotz offenen Bodens nur eine unerhört dürftige Unkrautvegetation.

Die Winterungen zusammenfassend sei gesagt, dass sich Raps 1958 als Förderer der herbstkeimenden Unkrautvegetation erwies, im Roggen hatte *Apera spica-venti* eine auffallende Häufigkeit, während übrige Winterannuelle in ihm eine gewisse Zurückhaltung zeigten. Auch im Weizen und Futterbau schien der Unkrautbesatz zu Beginn der Vegetationsperiode Deckungsgrade von 2 nur ausnahmsweise zu überschreiten.

Zu den verhältnismässig spärlich angetroffenen Arten gehörten vor allem folgende: *Aethusa cynapium*, *Arctium minus*, *Artemisia campestris*, *Camelina microcarpa*, *Cirsium vulgare*, *Daucus carota*, *Delphinium consolida*, *Erigeron canadense*, *Mentha arvensis*, *Stachys palustris*, *Teesdalia nudicaulis*, *Thlaspi arvense*, *Veronica opaca*, *polita* und *serpyllifolia*.

Sommeraspekt

Um zunächst über den Sommeraspekt der Winterungen zu berichten, sei angeführt, dass die fertilen Teile von *Cirsium arvense*, *Tripleurospermum maritimum* v. *inodorum*, *Rumex crispus* und *Artemisia vulgaris*, stellenweise auch *Papaver rhoeas* und *Centaurea cyanus* die Schotenschicht im Raps überragten und zur Samenentwicklung gelangten. Niedrige Arten starben nach Zusammenschluss der Kulturdecke auf den leichteren Böden weitgehend ab oder zeigte sich im übrigen ihre Entwicklung beim Räumen der Rapsfelder mehr oder weniger stark beeinträchtigt. Der üppige Zustand des Frühjahrs war vielerorts mit Ausnahme der kürzlich genannten Ueberwinterer einem dürftigen Kümern der Annuellen gewichen. Aus reichlichen Fruchtresten ging jedoch hervor, dass auch die meisten der niedrigen winterannuellen Arten zur Samenentwicklung gelangt waren. Zwischen den Resten der Frühjahrsvegetation waren sommerkeimende Arten wie *Chenopodium album*, *Polygonum* verschiedener Arten, *Matricaria matricarioides*, *Odontites rubra*, *Senecio vulgaris*, *Sinapis arvensis* und *Solanum nigrum* in beschränktem Umfang, meist als Zwergformen, aufgekommen.

Im Roggen konnte auf den nicht zu leichten Böden das Bild durch *Centaurea cyanus* und *Papaver rhoeas* fast ebenso farbenprächtig sein.

Die übrigen Papaver-arten traten hinter ihm zurück. An mehreren Lokalen war *Convolvulus arvensis* reichlich verbreitet, er trat, obwohl perenn, erst im Sommer in Erscheinung. *Apera spica-venti* gehörte zu den häufigsten und häufigsten Unkräutern im Roggen, auch auf leichtesten Böden. Sommerkeimer kamen in diesem Jahr nicht in nennenswertem Umfang zur Geltung, ein Zug, der verglichen mit Hackfrüchten auf gleichen Böden und in gleichen Lagen, bezeichnend war. Da im Sommergetreide die zuerst aufgekommene Unkrautvegetation durch chemische Bekämpfung mehr oder weniger beseitigt war, ergab sich, bedingt durch die Trockenheit im Juni—Juli, eine weitgehende Unkrautfreiheit in diesen Schlägen. Soweit ungespritzte Flächen von Sommergetreide, Fachs und Hülsenfrüchten angetroffen wurden, sind diese berücksichtigt, in einigen Fällen auch gespritzte Flächen. Für den Sommeraspekt der Unkrautflora in gespritzter Gerste sei folgendes Beispiel aus Saxtorp angeführt:

162/48 Kopf mit Örtlichkeit, Gerste D.gr. 2.

Boden: humusreicher, mittlerer Sand, pH 8,08 (August).

Datum: 14.6.1958.

Menge	Art	Entwicklungszustand
3—4	<i>Thlaspi arvense</i>	fertil, deformiert ¹
2—3	<i>Sinapis arvensis</i>	beginnende Blüte, deform.
3	<i>Spergula arvensis</i>	blüht, deformiert ¹
+	<i>Cirsium arvense</i>	Höhe der Gerste, deform. ¹
+	<i>Equisetum arvense</i>	steril 15—20 cm, deform.
2—3	<i>Polygonum convolvulus</i>	veget. Ranken, wenig geschädigt
+	<i>Scleranthus annuus</i>	Büschel, veget., „ „
1	<i>Polygonum persicaria</i>	10—20 cm, „ „
1	<i>Erodium cicutarium</i>	Rosetten „ „
+	<i>Viola arvensis</i>	blüht, „ „
+	<i>Artemisia vulgaris</i>	20 cm, stark deformiert
+	<i>Rumex acetosella</i>	blüht, deformiert

Bemerkung: *Veronica* in keiner Art vertreten.

Aus den oben angedeuteten Gründen wurde den Hackfrüchten, dem feldmässigen Gemüsebau, den Gemengen, dem Senf und Grünland besondere Aufmerksamkeit zugewendet, um die obligaten Sommerkeimer zu erfassen. Ihre Zusammensetzung kann aus folgenden Proben hervorgehen, wobei zu beachten ist, dass sämtliche angeführten Beispiele keinen Durchschnitt, sondern jeweils spezielle lokale Verhältnisse darstellen.

¹ (Fig. 6.)



Fig. 6. Einige durch chemische Bekämpfung mehr oder weniger geschädigte Unkräuter aus Weizen (2.6.1958). 1 *Cirsium arvense*, 2 *Tripleurospermum maritimum* var. *inodorum*, 3 *Lamium hybridum*, 4 *Capsella bursa-pastoris*, 5 *Veronica hederifolia*, 6 *Thlaspi arvense*, 7 *Spergula arvensis*. Die Keilzeichen weisen bei 3 auf Adventivwurzelbildung entlang des ganzen Stengels, bei 5 auf walzenförmige Stengelanschwellungen, bei 6 auf blasenförmige Stengelverdickungen. Zu den Arten, die nicht beeinträchtigt wurden, gehörte als auffallendste *Apera spica-venti*.

187/8 Kopf mit Örtlichkeit (Gemeinde Borgeby), feldmässige Möhre (Sorte ? London Torg), 30 cm hoch, D.gr. 3, pH 6,9, lehmiger humoser Sand.

- | | |
|------------------------------|-------------------------------|
| + <i>Senecio vulgaris</i> | + <i>Poa annua</i> |
| + <i>Lamium amplexicaule</i> | 1 <i>Solanum nigrum</i> |
| 1 <i>Urtica urens</i> | 2 <i>Chenopodium glaucum</i> |
| + <i>Polygonum aviculare</i> | + <i>Stellaria media</i> |
| 2 <i>Sonchus asper</i> | + <i>Linaria minor</i> |
| r <i>Chenopodium album</i> | r <i>Polygonum persicaria</i> |
| r <i>Taraxacum vulgare</i> | r <i>Rumex crispus</i> |

175/1 Kopf mit Örtlichkeit (nahe Lund), Zuckerrübe D.gr. 3, schwerer Lehm, pH 8,5 (Aug.).
Datum: 8.7.58.

- | | |
|---------------------------------|------------------------------|
| + <i>Veronica persica</i> | 2 <i>Fumaria officinalis</i> |
| + <i>Melandrium noctiflorum</i> | + <i>Galium aparine</i> |

+ <i>Cirsium arvense</i>	+ <i>Elytrigia repens</i>
+ <i>Equisetum arvense</i>	r <i>Matricaria matricarioides</i>
r <i>Chenopodium glaucum</i>	+ <i>Polygonum persicaria</i>
1 <i>Euphorbia helioscopia</i>	+ <i>Polygonum convolvulus</i>
1 <i>Euphorbia pepus</i>	+ <i>Polygonum aviculare</i>
r <i>Galeopsis speciosa</i>	+ <i>Polygonum tomentosum</i>
+ <i>Galeopsis ladanum</i>	+ <i>Chenopodium album</i>
r <i>Rumex crispus</i>	r <i>Solanum nigrum</i>
1 <i>Anagallis arvensis</i>	r <i>Papaver rhoeas</i>
r <i>Kickxia elatine</i>	+ <i>Lamium amplexicaule</i>
r <i>Viola arvensis</i>	+ <i>Sinapis arvensis</i>

224/32 Kopf mit Örtlichkeit (Gemeinde V. Karaby), Zuckermais D.gr. 2, loser humoser Sand, pH 6,3.
Datum: 24.7.58.

Sämtliche Arten sind mit dem Zeichen „+“ zu versehen (=auffallend üppig).

+ <i>Tripleurospermum mar. v. inodorum</i>	1 <i>Centaurea cyanus</i>
+ <i>Matricaria recutita</i>	1 <i>Chenopodium album</i>
r <i>Matricaria matricarioides</i>	+ <i>Anagallis arvensis</i>
+ <i>Anthemis arvensis</i>	1 <i>Arenaria serpyllifolia</i>
+ <i>Scleranthus annuus</i>	+ <i>Rumex acetosella</i>
1 <i>Elytrigia repens</i>	1 <i>Capsella bursa-pastoris</i>
+ <i>Veronica hederifolia</i>	r <i>Euphorbia helioscopia</i>
r <i>Veronica arvensis</i>	r <i>Spergula arvensis</i>
r <i>Solanum nigrum</i>	+ <i>Potentilla argentea</i>
r <i>Scabiosa arvensis</i>	r <i>Medicago lupulina</i>
r <i>Lamium amplexicaule</i>	+ <i>Galium aparine</i>
1 <i>Setaria viridis</i>	r <i>Apera spica-venti</i>
+ <i>Geranium molle</i>	+ <i>Thlaspi arvense</i>
+ <i>Geranium pusillum</i>	+ <i>Senecio vernalis</i>
2 <i>Erodium cicutarium</i>	+ <i>Erigeron canadense</i>
2 <i>Viola arvensis</i>	r <i>Equisetum arvense</i>
3 <i>Polygonum aviculare</i>	r <i>Anchusa arvensis</i>
2 <i>Polygonum convolvulus</i>	r <i>Papaver dubium</i>
r <i>Polygonum lapathifolium</i>	r <i>Myosotis arvensis</i>
r <i>Polygonum persicaria</i>	Gejätet, was aus zahlreichen vertrockneten Resten hervorgeht.

Auch ein Senf/Wickengemenge soll als Beispiel angeführt werden, da es den reichsten Bestand an *Chrysanthemum segetum* im ganzen Gebiet enthielt:

155/5 Kopf mit Örtlichkeit (nahe Lund), Wicken mit Senf als Stützfrucht, D.gr. Senf 2, Wicken 3.
Boden: sandiger Lehm, eben, pH 6,5.
Datum: 12.6.1958.

Menge	Art	Entwicklungszustand
2	<i>Polygonum persicaria</i>	Jungpflanzen
1	<i>Tripleurospermum maritimum</i> v. <i>inodorum</i>	"
+	<i>Sonchus arvensis</i>	c:a 5 cm Rosetten
2	<i>Cirsium arvense</i>	c:a 10 cm Rhizomtriebe
r	<i>Melandrium noctiflorum</i>	Erstarkungsstadium
+	<i>Galium aparine</i>	"
+	<i>Elytrigia repens</i> (<i>Triticum</i>)	Rhizomtriebe
+	<i>Polygonum amphibium</i>	kräftige Rhizomtriebe
+	<i>Stellaria media</i>	Blühbeginn
2	<i>Chenopodium album</i>	Keiml. u. Streck. st.
3*	<i>Chrysanthemum segetum</i>	Keim- u. Streckungsst.
+	<i>Veronica agrestis</i>	blüht, 10 cm
2	<i>Polygonum convolvulus</i>	rankt

Bemerkung: Nach Angabe des Eigentümers tritt *Chrysanthemum segetum* seit vielen Jahren auf und ist hier das lästigste Unkraut.

Die Unkrautbestände in den zahlreich inventierten Rüben und Kartoffeln wurden vornehmlich von folgenden Arten gestellt: *Anagallis arvensis*, *Anchusa arvensis*, *Arenaria serpyllifolia*, *Chenopodium album*, — *glaucum*, *Cirsium arvense*, *Convolvulus arvensis*, *Elytrigia repens*, *Equisetum arvense*, *Erodium cicutarium*, *Euphorbia helioscopia*, *Fumaria officinalis*, *Galium aparine*, *Lamium amplexicaule*, — *purpureum*, *Matricaria recutita*, — *matricarioides*, *Myosotis arvensis*, *Stellaria media*, *Tripleurospermum maritimum* v. *inodorum*, *Veronica*-Arten und *Viola arvensis*.

Die absolut wüchsigsten Unkrautbestände der Sommerungen kamen im Zuckermays und in einem Gurkensamenbau vor, sie erinnerten in ihrer Ueppigkeit an die Flora mancher ungestörter Ruderatplätze. Nur hier erschienen auch die im übrigen seltenen *Galinsoga parviflora* und *Solanum nitidibaccatum* (Fig. 7).

Auch Hülsenfrüchte enthielten eine eng begrenzte und für das Gebiet ungewöhnlichere Art in ausgiebiger Menge (Deckungsgrad 3—4) nämlich *Digitaria ischaemum*, die Feldfrucht war Gelblupine. Es machte den Eindruck, als ob dieses Gras eingesät worden wäre, was aber beim Fehlen jeglichen Futterwertes ausgeschlossen scheint. (Västra Karaby, Buchführungs-nr. 192/33.) Im übrigen waren die Hülsenfrüchte die unkrautfreisten Flächen, da sämtliche Erbsen, die auf riesigen Ländereien für die Konservenindustrie angebaut werden, ausnahmslos routinemässig gespritzt wurden. Sie zeigten auch normalerweise nach dem Gründrusch noch keinen Ansatz zur Herausbildung der lokalen Unkrautbestände.



Fig. 7. Als Seltenheit trat im untersuchten Gebiet u.a. *Solanum nitidibaccatum* in seinen beiden von einander stark abweichenden Typen auf.

Flachs enthielt stellenweise geringfügig *Sherardia arvensis* und meistens auch *Melandrium noctiflorum*.

Im Grünland traten im Sommeraspekt nur jene Unkräuter in Erscheinung, die dem Schnitt oder Beweiden entgangen waren, bzw. solche, die rasch Grundtriebe erzeugten: *Alchemilla arvensis*, *Anthemis arvensis*, *Arenaria serpyllifolia*, *Capsella bursa-pastoris*, *Cerastium holosteoides*, *Cirsium arvense*, *Erodium cicutarium*, *Equisetum arvense*, *Plantago*-Arten, *Scleranthus annuus*, *Stellaria media*, *Taraxacum vulgare*, *Tripleurospermum mar. v. inodorum*, *Tussilago farfara*, diverse *Veronica*. Dazu kamen noch in geringem Umfang *Lithospermum arvense*, sommerkeimende *Polygonum*, *Chenopodium*, *Sinapis*, *Centaurea* und *Anagallis*.

In sämtlichen Kulturen gehörte *Raphanus raphanistrum* überraschenderweise zu den Seltenheiten, während *Brassica campestris* überhaupt nicht verzeichnet werden konnte. Entweder war das Jahr nicht günstig

für diese Arten oder sind sie nun im untersuchten Gebiet weniger verbreitet. Nach Korsmo (6) ist *Raphanus raphanistrum* hauptsächlich ein Sommergetreidenunkraut. Die in diesen Kulturen gebräuchliche chemische Bekämpfung könnte sein geringes Vorkommen erklären, er hätte aber im Jugendstadium anzutreffen sein müssen. Nach Wehsarg (12) ist er eine Pflanze der ungaren, untätigen Böden. Diese sind im Gebiet wenig vorhanden. B. Granström (4) teilt 1955 mit, dass *Brassica campestris* im südlichsten Schweden nicht selten ist. Areschoug (1) bezeichnete sie im Jahre 1881 als verbreitet. T. Lagerberg (7) gibt dagegen an, dass Hederich und Ackersenf einander hierzulande anscheinend verbreitungsmässig ausschliessen. Boas (2) führt auf S. 105 an: „Der Hederich (*Raphanus raphanistrum*) bestreicht im saueren Bereich einen Raum von der Bodenzahl 18 (elende Sande) bis etwa zur Bodenzahl 72. In letzterem Falle handelt es sich um hochwertige, schwach saure Böden (Sandlehme, Braunerde). Sowie hier der Kalkhalt steigt, wird der Hederich sofort vom Ackersenf abgelöst“. (S. 183 werden beide „antipodiale Landschaftsdeuter“ genannt.) Auffällig war, dass *Agrostemma githago* in sämtlichen Früchten gänzlich fehlte.

Eng begrenzte Vorkommen von *Kickxia elatine*, *Euphorbia exigua* und *Sherardia arvensis* lagen in verschiedenen Sommerfeldfrüchten der Gemeinden Fjellie, Stävie und Barsebäck. Sie scheinen kolloidreichere Böden zu bevorzugen. An einer Stelle ist, wie erwähnt, erst im Spätsommer (September) sowohl im Feldinneren als auch in den Rainen *Galinsoga parviflora* aufgetaucht. Dieses Unkraut der Gärten und Schuttplätze scheint hier noch nicht in grösserem Umfange in den Ackerbau übergetreten zu sein. (Auf einem vernachlässigten, abgeernteten Gemüsefeld ausserhalb des Untersuchungsgebietes, bei Hälsingborg, dominierte dieses Unkraut mit Deckungsgraden bis 5 über sämtliche anderen Unkräuter im November!) Dagegen dürfte nach den vorliegenden Anzeichen *Matricaria matricarioides* schon zu den bodenständigen Ackerbaubegleitern des Feldinneren, nicht nur der Trittflächen, zu rechnen sein, soweit einjährige Beobachtungen eine solche Vermutung zulassen. Nach Wehsarg (12) ist sie in Deutschland auf dem Wege, eine Vermehrung des Ackerunkrautsortimentes, besonders der Hackfrüchte, zu werden.

Zusammenfassung

Im Jahre 1958 wurde in 16 Gemeinden des Gebietes zwischen Lund und Landskrona (Schweden) eine Erhebung über die Ackerunkrautflora durchgeführt. Die Anzahl der festgestellten Arten betrug 180, ihre Verbreitung wurde nach dem Verfahren von Braun-Blanquet erfasst und u.a. zu einer Tabelle zusam-

mengeställt. Höchste Frekvenzen bei jedoch niedrigen Deckungsgraden lagen för *Viola arvensis* vor, den höchsten vorherrschenden Deckungsgrad mit zugleich sehr hohen Frekvenzen wies *Apera spica-venti* auf. Die artenreichste Gattung war *Veronica*, die mit 8 Arten vertreten war.

Sammanfattning

1958 genomfördes i 16 västskånska socknar en inventering av åkerogräsvegetationen. För varje socken utsågs ett antal inventeringsytor, som fördelade sig på olika grödor och i förekommande fall på olika jordarter. Ogräsbestånden noterades till art och mängd, uppgifterna sammanfördes i en tabell.

Av de 180 anträffade ogräsarterna är inte alla typiska för brukade ytor, eftersom en del fanns framför allt eller enbart på trädesåkrar. Det mest artrika släktet, *Veronica*, uppträdde med 8 arter. De företagna undersökningarna lämnade bl.a. följande resultat.

Ogräsen i raps kunde nå kraftigare utveckling än i andra grödor på jämförbar jord, vilket förmodligen kan tydas som ett utslag av kvävetillgången.

Följande arter utgjorde områdets allmännaste åkerogräs (med frekvenser överstigande 30 %): åkerven *Apera spica-venti*, sandnarv *Arenaria serpyllifolia*, lommeört *Capsella bursa-pastoris*, blåklint *Centaurea cyanus*, kvickrot *Elytrigia repens*, åkerförgätmigej *Myosotis arvensis*, kornvallmo *Papaver rhoeas*, vitgröe *Poa annua*, trampört *Polygonum aviculare*, våtarv *Stellaria media*, baldersbrå *Tripleurospermum maritimum* v. *inodorum*, murgrönsveronika *Veronica hederifolia* och åkerviol *Viola arvensis*. Av nämnda arter äger åkervenen speciellt intresse, då vissa omständigheter tyder på att den håller på att expandera.

Sprutade spannmålsodlingar och mörgrarter samt rotfrukter var relativt fria från ogräs (dock förekom åkerven *Apera spica-venti*, i höstsåden).

Sockermajs och viss fältmässig köksväxtodling hörde till de ogräsrikaste arealerna.

Förekomsten av åkerrättika *Raphanus raphanistrum* jämfört med åkersenap *Sinapis arvensis* var obetydlig inom området, medan åkerkål *Brassica campestris* ej anträffats. Ej heller har klätt *Agrostemma githago* iaktagits.

Av »nya» ogräsarter har kanadabinka *Erigeron canadense* observerats sporadiskt, och gängel *Galinsoga parviflora* tillhörde i ett fall åkerytans inre vegetation, medan förekomsten av gatkamomill *Matricaria matricarioides* tyder på att detta ogräs hävdar sig i icke obetydlig omfattning även på från kanter och vägar långt avlägsna lokaler i grödorna.

Vårkorsört *Senecio vernalis* förekom relativt rikligt.

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- (11) WALTER, HEINRICH, Einführung in die Phytologie, IV, Grundlagen der Vegetationsgliederung, von HEINZ ELLENBERG. Stuttgart 1956.
- (12) WEHSARG, OTTO, Ackerunkräuter. Berlin 1954.

Pflanzenart	Gemeinde												Gebietsfrequenz
	1	2	3	4	5	6	7	8	9	10	11	12	
<i>Achillea millefolium</i>	1	+	+	+	+	+	+	+	+	+	+	+	8,3
<i>Aethusa cynapium</i>	3	+	+	+	+	+	+	+	+	+	+	+	4,3
<i>Aira praecox</i>	7	+	+	+	+	+	+	+	+	+	+	+	0,3
<i>Anagallis arvensis</i>	+	+	+	+	+	+	+	+	+	+	+	+	11,0
<i>Anchusa arvensis</i>	+	+	+	+	+	+	+	+	+	+	+	+	4,7
<i>Anchusa officinalis</i>	+	+	+	+	+	+	+	+	+	+	+	+	1,0
<i>Anthemis arvensis</i>	2	+	+	+	+	+	+	+	+	+	+	+	32,3
<i>Anthoxanthum odoratum</i>	4	1	5	+	+	+	+	+	+	+	+	+	0,3
<i>Apera spica-venti</i>	1	+	+	+	+	+	+	+	+	+	+	+	40,0
<i>Aphanes arvensis</i>	1	+	+	+	+	+	+	+	+	+	+	+	14,0
<i>Arabis thaliana</i>	1	+	+	+	+	+	+	+	+	+	+	+	22,0
<i>Arctium minus</i>	7	+	+	+	+	+	+	+	+	+	+	+	2,0
<i>Arenaria serpyllifolia</i>	4	+	+	+	+	+	+	+	+	+	+	+	49,0
<i>Artemisia vulgaris</i>	4	+	+	+	+	+	+	+	+	+	+	+	12,0
<i>Artemisia campestris</i>	3	+	+	+	+	+	+	+	+	+	+	+	2,0
<i>Avena fatua</i>	1	+	+	+	+	+	+	+	+	+	+	+	4,0
<i>Barbarea vulgaris</i>	1	+	+	+	+	+	+	+	+	+	+	+	0,7
<i>Bellis perennis</i>	1	+	+	+	+	+	+	+	+	+	+	+	0,3
<i>Berteroa incana</i>	1	+	+	+	+	+	+	+	+	+	+	+	1,3
<i>Bromus arvensis</i>	1	+	+	+	+	+	+	+	+	+	+	+	0,3
<i>Bromus inermis</i>	1	+	+	+	+	+	+	+	+	+	+	+	0,3
<i>Bromus mollis</i>	2	1	+	+	+	+	+	+	+	+	+	+	1,3
<i>Bromus secalinus</i>	1	+	+	+	+	+	+	+	+	+	+	+	1,0
<i>Bromus tectorum</i>	1	+	+	+	+	+	+	+	+	+	+	+	0,3
<i>Cakile maritima</i>	1	+	+	+	+	+	+	+	+	+	+	+	0,6
<i>Camelina microcarpa</i>	1	+	+	+	+	+	+	+	+	+	+	+	1,3
<i>Campanula rapunculoides</i>	21	+	+	+	+	+	+	+	+	+	+	+	0,3
<i>Capsella bursa-pastoris</i>	4	+	+	+	+	+	+	+	+	+	+	+	47,0
<i>Carduus crispus</i>	12	+	+	+	+	+	+	+	+	+	+	+	0,3
<i>Gentaurea cyanus</i>	3	+	+	+	+	+	+	+	+	+	+	+	45,0
<i>Gentaurea rhénana</i>	1	+	+	+	+	+	+	+	+	+	+	+	0,6
<i>Gentaurea scabiosa</i>	1	+	+	+	+	+	+	+	+	+	+	+	0,6
<i>Cerastium arvense</i>	1	+	+	+	+	+	+	+	+	+	+	+	0,6

(Forts.)

(Forts.)

Galium aparine	20	+	4	+	3	+	9	+	4	+	1	+	1	+	4	1	1	6	+	1	+	5	+	—	—	4	2	7	+	1	+	24,0		
Geranium dissectum	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3		
Geranium molle	2	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3,7		
Geranium pusillum	7	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14,0		
Glechoma hederacea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3		
Gnaphalium uliginosum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,0		
Helianthus tuberosus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3		
Helichrysum arenarium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3		
Herniaria glabra	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,6		
Hieracium dubium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,6		
Holcus lanatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,6		
Hypericum perforatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3		
Hypochoeris glabra	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3		
Jasione montana	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,6		
Juncus bufonius	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,0		
Kickxia elatine	3	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,0		
Knautia arvensis	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,3		
Lactuca serriola	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3		
Lanum album	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,6		
Lanum amplexicaule	13	+	4	+	5	+	6	+	9	+	6	+	4	+	4	+	1	+	3	+	1	+	10	+	2	+	4	+	9	+	3	+	28,0	
Lanum hybridum	8	+	2	+	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6,3	
Lanum purpureum	5	+	1	+	9	+	3	+	6	+	5	+	2	+	4	+	2	+	5	+	—	—	—	—	—	—	—	—	—	—	—	—	19,0	
Lapsana communis	3	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,0		
Linaria vulgaris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,6		
Liliospermum arvense	4	+	2	+	1	+	4	+	1	+	2	+	8	+	3	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18,0	
Lolium perenne	2	+	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2,6	
Luzula campestris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3		
Lysimachia nummularia	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3		
Malva neglecta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1,0		
Matricaria recutita	3	+	2	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10,0	
Matricaria matricarioides	7	+	2	+	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7,3	
Medicago lupulina	3	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2,7	
Medicago sativa	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3	
Melandrium album	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3	
Melandrium noctiflorum	12	+	2	+	3	+	2	+	3	+	6	+	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15,0
Mentha arvensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5,0	
Myosotis arvensis	10	+	2	+	11	+	7	+	10	+	13	+	4	+	4	+	6	+	16	+	8	+	20	+	4	+	1	+	9	+	6	+	46,0	
Myosotis stricta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8,0	
Myosurus minimus	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11,7	
Odonites rubra	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3,3	
Oenothera biennis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,3	
Papaver argemone	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9,0	

(Forts.)

[illegible]

Studies in the Genus *Laminaria*

I. *Laminaria cuneifolia* J. G. Agardh: A Review

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The genus *Laminaria* has been recognized as a taxonomically problematic group for some time. Although clear well-defined species exist, they represent only a small minority of the total number of species contained within the genus. There has been little agreement over the remaining majority of species, each author presenting a list differing in both length and content from those prepared for the genus by other investigators. All who have seriously attempted to identify the species using even the best existing keys must be aware that the present taxonomic treatments of *Laminaria* are inadequate. Those who have done original work in the group not only recognize the need for further study of these confusing plants but also know something of the many difficulties involved in such work. The problems of identity and relationship of a great number of species of *Laminaria* still remain a challenge.

The taxonomic problems within the genus *Laminaria* became increasingly interesting to me during the course of my field studies and subsequent laboratory analyses of marine algal collections from the northeastern provinces of Canada.¹ Since June, 1958 I have been able to visit the major European herbaria and continue my field work in the Norwegian Arctic (summer, 1958) for the purposes of examining important historical Arctic algal collections and comparing the Canadian and European Arctic marine floras. During these studies, still in pro-

¹ These collections were made in New Brunswick (Gaspé Peninsula), Nova Scotia, including Cape Breton Island, in northern Newfoundland, southern and eastern Ungava Bay, Quebec, southeastern Baffin Island, and along the entire coast of Labrador. A total time of twelve months was spent in the field, spread over the ice-free seasons of 1954, 1955, 1956 and 1957.

gress, special attention has been given to the members of the genus *Laminaria*.

I do not wish to discuss the taxonomy of the entire genus nor of the whole group of the North American species at this time. This paper will be concerned only with the problems relating to *Laminaria cuneifolia* J. G. Agardh. At the completion of my studies in the European herbaria and after field work during the summer of 1959 in Grenland, I hope to discuss in detail in future papers all of the species we have or have had attributed to our northeastern coast of North America.

My attention was attracted to *Laminaria cuneifolia* J. G. Agardh when I recently discovered that Kützinger had described a species by this name in 1843. Since according to the rules of nomenclature Agardh's name, published twenty-four years later in 1867, is illegitimate, I began searching for another name to replace it, a simple task I thought for what seemed to be a rather clearly defined species reported only from several widely separated regions of the north. The problem was more complicated than it first appeared, however, leading me somewhat far afield and it has become necessary to include references to many of the taxonomic studies on other *Laminaria* species from northern waters as well as a discussion of the pertinent collections. I shall defer for the moment the problem of Kützinger's plant and the changing of the name of *L. cuneifolia* J. G. Agardh, for this has become subordinate to a larger problem concerning the nature of Agardh's species. It would be well to begin with the original description of *L. cuneifolia* J. G. Agardh, which I have given below:

LAM. CUNEIFOLIA (*J. Ag. mscr.*) radice fibrosa, ramis fibrarum ultimis sensim tenuioribus, stipitem solidum teretiuseculum brevem sustinente, fronde transverse biserialiter bullata, soro supra basem laminae maculam (majorem) in disco expansam efficiente.

Laminaria latifolia C. Ag. *sp. partim* (quoad specim. Kamtschatka) et *exclus. synon.*

Laminaria saccharina forma *cuneata*, Post et Rupr. Illustr. Alg. p. 10.

Laminaria saccharina var. *latifolia* Rupr., Alg. Ochot. p. 351!

Hab in oceano pacifico septentrionali as oras Asiae et Americae.

The species given as the first synonym by J. G. Agardh, *Laminaria latifolia* C. A. Agardh (1822, p. 119), is itself based upon three entities, two of which were excluded by the younger Agardh from his *Lam. cuneifolia*. Those two excluded are the synonyms cited by C. A. Agardh, *Ulva maxima* Gunn. (Fl. Norv., 1772, II, t. 7, f. 5) and *Fucus saccharinus* var. *latissimus* Turn. (Hist., 1811, p. 69), described from collec-

tions made in Norway and the British Isles respectively. Only the third element of *Laminaria latifolia* was collected from a region that might be considered arctic or subarctic and, significantly, it is this element which J. G. Agardh placed in his new species. This component of Agardh's *Lam. cuneifolia* is represented by a single collection from the west coast of the Kamtschatkian Peninsula and attributed by the senior Agardh to Tilesius (C. A. Agardh, 1822, p. 119). There are two rather poorly preserved specimens of the Tilesius collection¹ in the Agardh herbarium at Lund. The stipe of each plant is short, less than 3 cm., terete throughout most of its length but complanate near its junction with the blade. In neither specimen are mucilage canals to be found in the stipe. The blades, rather complete except for the upper portion of one, measure 33 cm. by 17 cm. and 75 cm. by 18 cm. The blade has a sharply cuneate base in both plants, then expanding very gradually upwards, the margins becoming slightly ruffled. The entire blade has a papery texture and is light olive to olive-brown in color. According to the modern type concept, these two specimens must be regarded as syntypes.

Laminaria saccharina forma *cuneata* Post. et Rupr., the second synonym given for *Lam. cuneifolia*, is based upon plants collected from the most northwestern coasts of North America by Alexander Postels and Henery Mertens during the Lütke Expedition² in 1827 and 1828. No specimen from this collection is in the Agardh herbarium, the herbarium at Leningrad nor in the other herbaria in which I have searched for these plants. I have not, therefore, had the opportunity to examine this element of J. G. Agardh's species.

The last of the three synonyms cited by J. G. Agardh, *Laminaria saccharina* var. *latifolia* Ruprecht (1851, p. 351), is based upon specimens collected by Hr. V. Middendorff and H. Wosnessenski from the largest of the Schantar Islands near Cap Nicha, eastern Mare Ockotsh. Although there are earlier collections from the region of Mare Ockotsh, e.g. those of W. von Merck, Tilesius, Horner, Chamisso and Wormskiold, all probably containing specimens of *Laminaria*, Ruprecht discusses only those of Middendorff and Wosnessenski taken at the mouth of the Uda River, as he feels "certain of the localities". The specimens of *Lam.*

¹ Probably from Avatche Bay, as Tilesius visited Petropavlovsk in July and September of 1804 and in June, August and November of 1805.

² These botanists aboard the corvette "Senjavin" with Captain Lütke visited Sitka from June 24 to July 31, 1827 and later stopped at Unalaska, the Pribilof Islands and St. Matthew Island in the northern Bering Sea.

saccharina var. *latifolia*, along with those of the Postels-Mertens collection, make up the remainder of the syntypes of *Lam. cuneifolia* J. G. Agardh. I have seen two of these specimens annotated by Ruprecht, one in the Riksmuseum, Stockholm, and one in Agardh's herbarium. The plants are much alike with short, terete stipes and blades with a cuneate base and expanding only slightly and gradually upwards. In both plants mucilage canals are present in the stipe as well as the blade. Agardh also has in his herbarium a specimen from the same collection, determined by Ruprecht as *Laminaria saccharina* var. *lessoniaefolia*, a name Ruprecht never published. He refers indirectly to the plant as merely a "form" which is intermediate between *Lam. saccharina* var. *latifolia* and *Lam. saccharina* var. *linearis* (Ruprecht, 1851). This "intermediate form" differs from var. *latifolia* only in having a more extremely narrow cuneate blade base. There is no difference anatomically between this specimen and Agardh's specimen of var. *latifolia*, yet he did not include it as a member of his new species *Lam. cuneifolia*.

None of the syntypes of *Lam. cuneifolia* J. G. Agardh I have seen, either in his own herbarium or in Stockholm, are designated by this species epithet, but are to be found bearing the names by which they were cited in the description of his species. There are, however, in Agardh's herbarium, two specimens annotated by him as *Lam. cuneifolia*. Although the dates on these specimens make it quite possible that they were in his possession at the time the description was written, he did not cite them and they cannot be included among the syntypes. Nevertheless they should be discussed, for they add to our knowledge of Agardh's own concept of *Lam. cuneifolia*. One of them, bearing the data "Terre-neuve, 1828, Despréaux" and originally identified as *Laminaria saccharina* (L.) Lamourx., shows no evidence of mucilage canals in the stipe. In its other characters it agrees with the description of *Lam. cuneifolia*. The second specimen is also a North American plant, collected at Esquimalt, a small harbor just west of Victoria, B. C., Canada. It was identified and cited by W. H. Harvey (1862, p. 166) as *Lam. saccharina*. The plant has a short stipe, mostly terete and an undivided blade with a sharply cuneate base. Mucilage canals occur in both the stipe and the blade. It differs in general appearance from all the other plants thus far discussed; it is dark in color and coriaceous in texture. It is much like, if not exactly comparable to what Setchell and Gardner (1925, p. 602) describe as *Laminaria cuneifolia* f. *subsimplex*. I will discuss this plant in relation to those of Setchell and Gardner later in this paper. Also in the Agardh herbarium is a collection made by Pro-

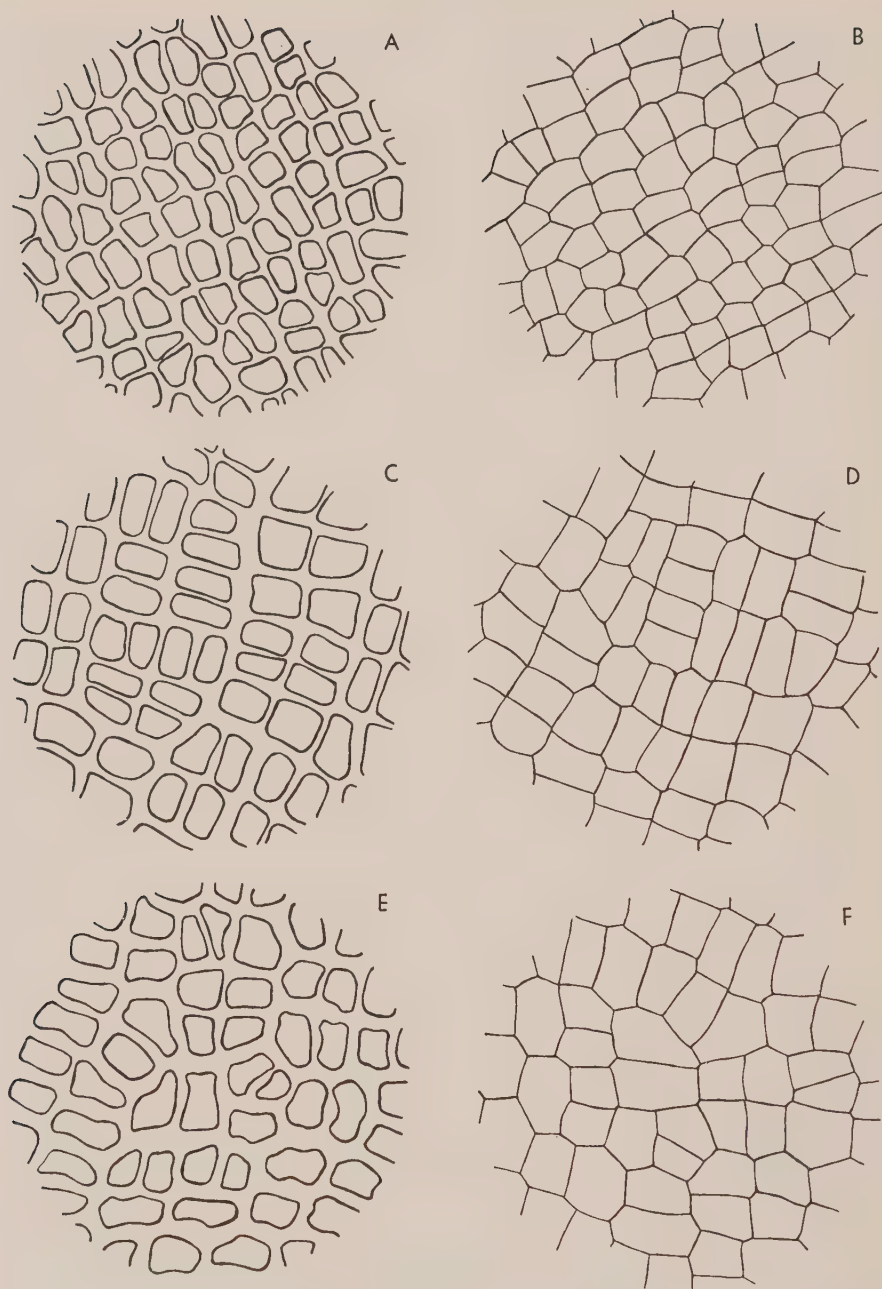


Fig. 1. (A—B) *Lam. groenlandica* Rosenv. (C—D) *Lam. cuneifolia* J. G. Ag. (Berggren collection). (E—F) *Lam. saccharina* var. *latifolia* Rupr. $\times 610$. — All figures are of the surface view of the outer most cortical cells and their protoplasts as seen in the mature regions of the blade of soaked herbarium material. In each figure the outline of the cells are drawn to the right and their corresponding protoplasts arranged to the left of the page.

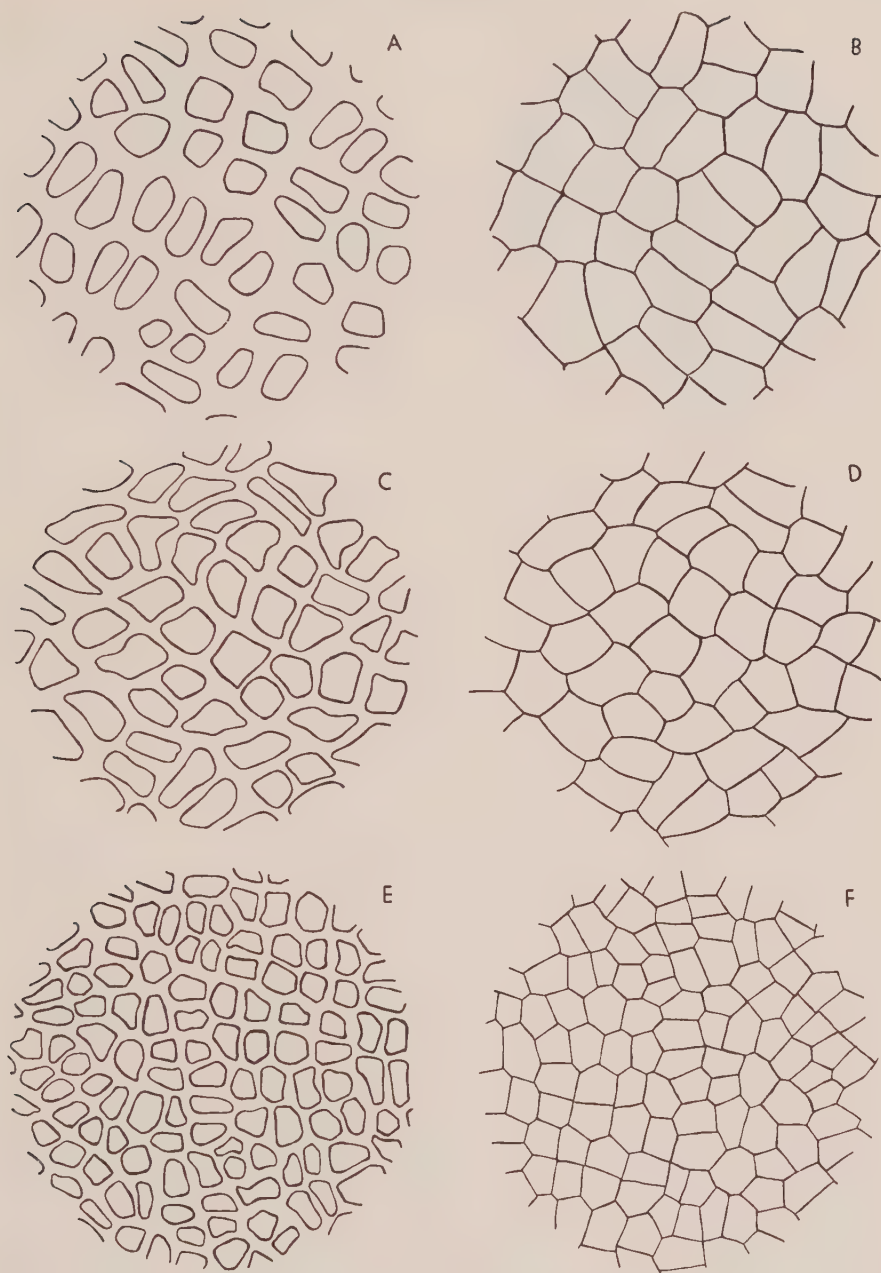


Fig. 2. (A—B) *Lam. cuneifolia* J. G. Agardh (Kjellmans' collection). — (C—D) *Lam. latifolia* C. Agardh. (E—F) *Lam. cuneifolia* Kützinger (young specimen). — $\times 610$.

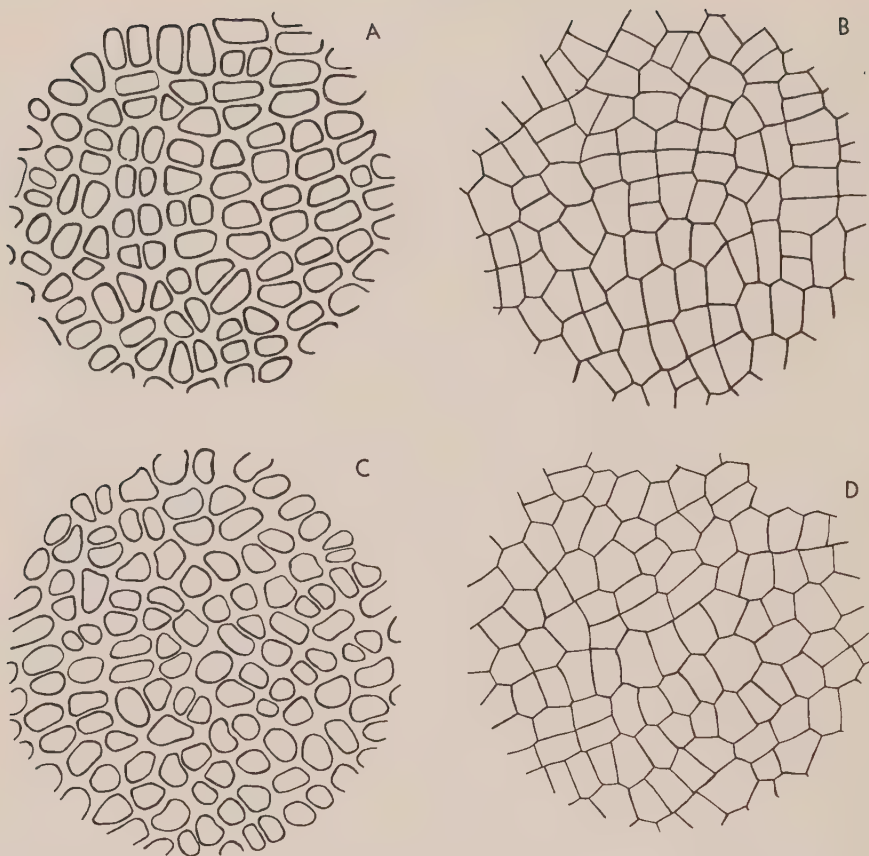


Fig. 3. (A—B) *Lam. cuneifolia* "Esquimalt" collection. (C—D) *Lam. cuneifolia* f. *subsimplex* Setch. et Gard. — $\times 610$.

fessor Sven Berggren and P. Öberg of Lunds Universitet at Jakobshavn, west Greenland, just south of Disko Island, which Agardh (1870, 1872) regarded as *Lam. cuneifolia*.

After a careful study of the available syntypes (four specimens) and the annotated but uncited specimens mentioned above, I must conclude that the syntypes and the "Terre-neuve" specimen and the Berggren collection in reality include two anatomically distinct but morphologically very similar species, while the single "Esquimalt" specimen from British Columbia proves to represent still a third species. Before mentioning the differences by which these species may be distinguished from each other, it might be well to recall their similarity. All of these plants have short terete stipes and undivided blades with a cuneate base.

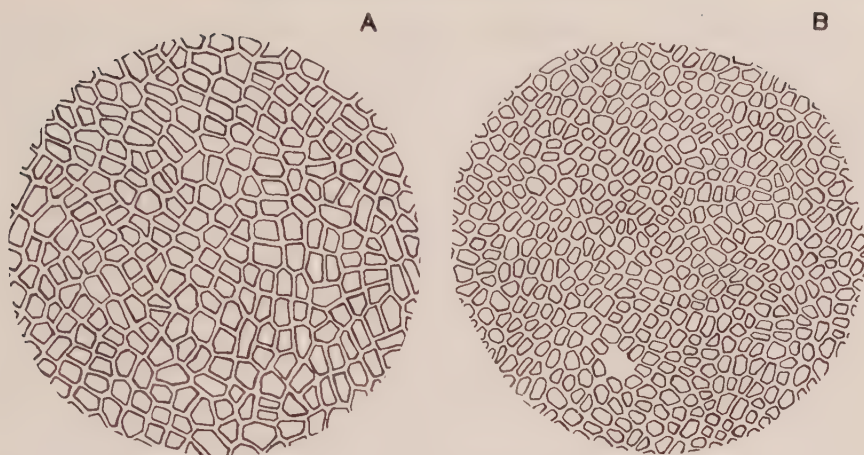


Fig. 4. (A) *Lam. saccharina* var. *latifolia* Rupr. (B) *Lam. cuneifolia* f. *subsimplex* Setch. et Gard. — $\times 270$.

The blade, above the cuneate base, broadens very slightly and gently upwards, becoming somewhat ruffled on the margins in some instances. It is possible to separate these plants easily into two groups depending on the presence or absence of mucilage canals in the stipe. The group lacking these canals in the stipe, to which belong the Kamtschatka specimens of *Lam. latifolia* C. A. Agardh and the "Terre-neuve" specimen, must be referred to *Lam. saccharina* (L.) Lamourx., for *Lam. cuneifolia* J. G. Agardh has mucilage canals described for both stipe and blade.¹ The second group, which conform to Agardh's description, contains the specimens of *Lam. saccharina* var. *latifolia* Rupr., the Berggren collection, and the single "Esquimalt" specimen. The latter specimen, however, is distinct from all of the others of both groups, its differing not only in color and texture as previously mentioned, but in the size, shape and arrangement of the surface cells² as seen in surface view, and in the same respects, the appearance of the protoplasts (Fig. 3 A—B). The "Esquimalt" plant is dark brown to black and coriaceous in contrast to the light olive to olive-brown color and the papery texture of all the specimens of both typical *Lam. cuneifolia* and *Lam. saccharina*. The presence of mucilage canals in both the stipe and blade easily separates it anatomically from *Lam. saccharina*. The distinctive char-

¹ "Canales muciferi in stipite adsunt, evidentes, tamen minuti et parum conspicui (nec magni ut in *L. solidungula*).\" J. G. Agardh, 1867, p. 11.

² Those cells that make up the outermost layer of the cortex.

acter of the surface cells of the "Esquimalt" plant perhaps most readily separates it from the other two species (Fig. 1—4). In the mature regions of the blade (i.e. neither close to the margins of the blade nor to the primary meristem) the surface cells of both *Lam. saccharina* and *Lam. cuneifolia* (also *Lam. groenlandica*) are mostly pentagonal to hexagonal in surface view, ranging from 55 μ to 90 μ in diameter and arranged roughly in uneven parallel series. The surface cells of the "Esquimalt" specimen, however, are always about one-third smaller in diameter (Fig. 4 A—B), and are most frequently arranged into groups of four, although occasionally showing a tendency toward the parallel arrangement. The number of cell walls seen in surface view are the same for the cells of both groups of plants, and each are seen to be distinctly angular with oil immersion. Under 10 \times and 45 \times objectives, however, the characteristic bead-like appearance of the protoplast of the surface cells of the "Esquimalt" type are easily distinguishable from the larger, more angular protoplasts found in the other plants. Under lower magnification the two shapes are more difficult to distinguish when working from preserved or soaked dried material. Thus, although it has the correct distribution of canals in the stipe and blade as well as conforming to the general shape of *Lam. cuneifolia* J. G. Agardh, the "Esquimalt" specimen has so many distinguishing characters that I prefer to regard it as separate from that species.

Setchell and Gardner (1910, p. 257; 1925, pp. 600—603) and Setchell (1912, p. 151) discuss a plant which they refer to *Lam. cuneifolia* J. G. Agardh and to which they attribute a distribution of from St. Lawrence Island, Alaska to Puget Sound, Washington. I have studied a number of specimens from northwest North America annotated and widely distributed by these authors as *Lam. cuneifolia*. I cannot consider them as members of that species, for these plants in every respect correspond to the "Esquimalt" specimen in the Agardh herbarium. Setchell had seen this specimen, one of the two that Agardh actually annotated as *Lam. cuneifolia*, and this is doubtless why he included the North American west coast plants under Agardh's species. It is interesting that concerning the Berggren collection, regarded by Agardh himself as representative of his species, Setchell and Gardner (1925, p. 601) wrote that it "... seems to be a different species and is closely related to *Lam. groenlandica* Rosenvinge." These authors have obviously accepted the "Esquimalt" specimen to represent *Lam. cuneifolia* while they regard the real *Lam. cuneifolia* to be a different species, although just the reverse is actually the case.

The misunderstanding of this species has naturally led to some confusion in the distribution records. In 1903 Setchell and Gardner gave the distribution of *Lam. cuneifolia* unchanged from Agardh's original description but with the addition of one more recent record by Saunders (1901, p. 429) from Popof Island, one of the Shumagin group of the eastern Aleutians. They cited this record with reservation as they were "... uncertain of the latter's [Saunders'] determination." It is impossible to tell without having seen Saunders' specimen whether those he refers to *Lam. cuneifolia* really belong to that species or not, for he makes no reference to the anatomy of the stipe. The description accompanying the plants that he refers to *Lam. saccharina* forma *a* however, leaves no question that these are certainly not *Lam. saccharina* but most likely *Lam. cuneifolia* J. G. Agardh.

By 1925 Setchell and Gardner had completely revised their concept of Agardh's species to include in it *Lam. bullata* Kjellman and all the American west coast forms that they had previously attributed to the latter species (1903, 1912). While their revision of *Lam. cuneifolia* enlarged the species in one way, it narrowed the species drastically in another to the exclusion of all the plants from Greenland, the Siberian Arctic, and other regions of the far north. Although they have recognized that the type may be from Mare Ochotsk, "Agardh makes no statement as to type, but probably regards the Ochotsk Sea plants from that point of view.", they chose *one* of the specimens annotated by Agardh as representative of this species . . . the "Esquimalt" specimen not one of the syntypes. Thus, in one sense, they not only excluded from Agard's species all the plants from the above mentioned regions of the arctic, but they also completely misinterpret the collections that Agardh originally based his species upon, upon which Agardh based his species originally! They remain uncertain as to the nature of the Alaskan plant attributed by Saunders (1901, p. 429) to *Lam. cuneifolia*, making no reference to the anatomy of the stipe and blade but imply that the external features of this plant do not agree with the "Esquimalt" type specimen. They therefore exclude this record from their synonymy. Their misinterpretation of *Lam. cuncifolia* has thus led them to attribute to this species a much more southern distribution than what seems actually to be the case.

Although it is clear that the American west coast plants referred to *Lam. cuneifolia* by Setchell and Gardner and the "Esquimalt" specimen do not belong to Agardh's species at all, the question as to what species they do belong is still open. Setchell and Gardner combine the west

coast plants and *Lam. bullata* Kjellm. with certain reservations, as the latter is “. . . probably better reckoned in the digitate section,” and “. . . *Lam. cuneifolia* is more typical of the ‘saccharina’ group.” Nevertheless they treated *Lam. bullata*, combined with the west coast ‘cuneifolia’, under *Simplices Section*, saying that there are several species in this section which seem to exhibit naturally both the digitate and entire conditions of the blade. As an example of such a species they give only *Lam. cuneifolia*. It is not uncommon for a member of the *Digitate Section* to manifest entire blades, but I have never encountered a species in the *Simplices Section* that showed any tendency toward naturally occurring division, nor have I ever seen a reference to such a phenomenon except for that by Setchell and Gardner. As Kjellman (1889, p. 40) described *Lam. bullata* it belongs to the *Digitate Section* even though his plate (Pl. 2, fig. 5) shows an immature plant with an undivided blade. The majority of specimens of this species from Kjellman’s “Vega” Expedition collections (deposited at Uppsala, Stockholm and Lund) show clearly that the blade is usually divided into a few, or in some cases, numerous segments. Even in the mature plants with apparently undivided blades there is at the apex of the blade some evidence of a former segmentation.

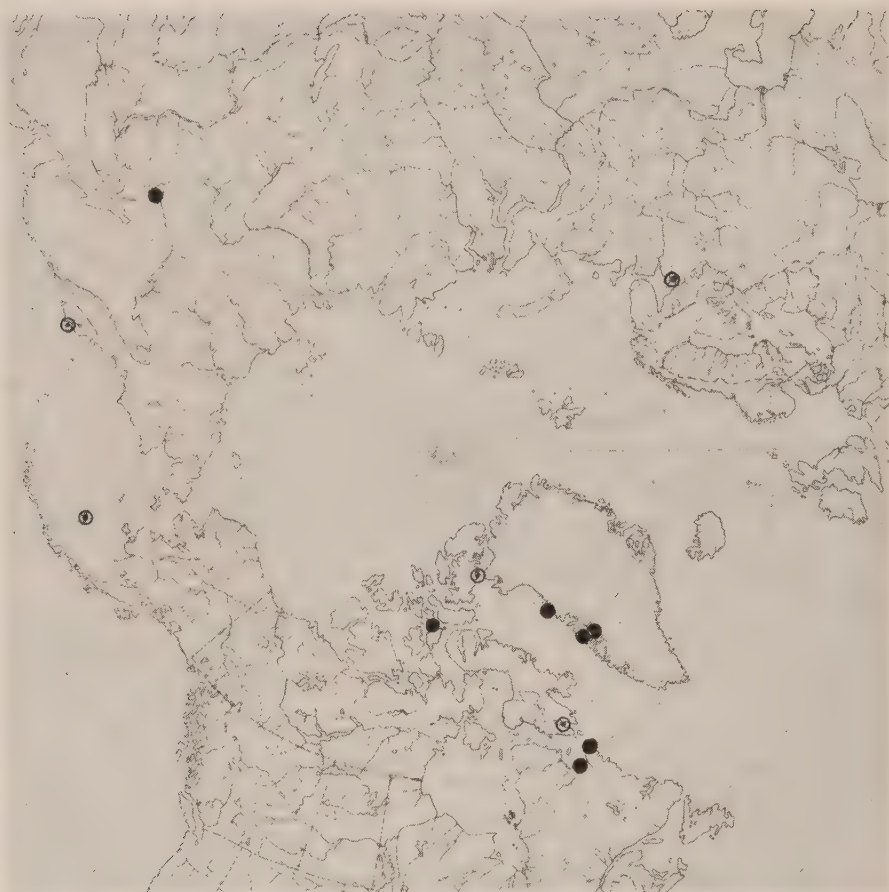
I have not as yet had the opportunity to study a sufficient number of specimens of Setchell and Gardner’s west coast plant to permit a deeper analysis of their identity and relationships to the other species of *Laminaria*. They seem, however, to be related to Kjellman’s *Lam. bullata* and may constitute a north Pacific species with a center of distribution possibly in the region of the Bering Sea extending southwards along the coasts of northeastern Asia and northwestern America. A similar species complex of digitate *Laminaria* having mucilage canals in the stipe and blade is present in the northeastern American arctic, Greenland and the high European arctic marine environments, (e.g. Spitsbergen). The problems of relationship and identity will be pursued further and discussed in a later study of the digitate members of the Genus *Laminaria*. It is sufficient for the purposes of the present investigation to show that these plants should be excluded from *Laminaria cuneifolia* J. G. Agardh.

Since J. G. Agardh’s *Lam. cuneifolia* has proven to be a good, albeit somewhat misunderstood species, it is unfortunate that the name he applied to it should be illegitimate according to our present rules. The name *Laminaria cuneifolia* was validly and effectively published by Kützting (1843, p. 355; 1849, p. 575) for specimens he collected and de-

scribed from Helgoland (July 1839, Wird his 1' gross"). It is difficult to understand why J. G. Agardh, who must have been cognizant of Kützing's collection, and the name attached to them, made no reference to the two descriptions of Kützing's mentioned above. Perhaps he suspected, and correctly so, that Kützing's plants from Helgoland represent one of the many forms of *Lam. saccharina* (L.) Lamourx., as did De Toni (1895, p. 345), who lists Kützing's species under his "species maxime dubiae" and claims "non J. G. Agardh."¹ I have had an opportunity to study Kützing's collection in Leiden which contains a rather large number of small *Laminaria* specimens in an excellent state of preservation, and I find that they agree in all respects with what is today usually referred to *Lam. saccharina*. Not only does their anatomy eliminate them from *Lam. cuneifolia* J. G. Agardh, but their locality, Helgoland, appears to be well outside the southern limit of the range of Agardh's species, which is without doubt a cold-water species. Thus it is impossible to regard *Lam. cuneifolia* J. G. Agardh as synonymous with Kützing's earlier species of the same name.

At present there is some doubt in my mind that *Lam. groenlandica* Rosenvinge (1893, pp. 847-848) is distinct from *Lam. cuneifolia* J. G. Agardh. In his descriptions and discussions of *Lam. longicruris* De la Pyl., *Lam. cuneifolia* J. G. Agardh and *Lam. groenlandica*, Rosenvinge (1893, pp. 845-849) himself questions whether the latter two species might not be growth forms or stages in the development of *Lam. longicruris* De la Pyl. He does not suggest the more likely possibility that *Lam. cuneifolia* and *Lam. groenlandica* are distinct from *Lam. longicruris* but not from each other. I have no doubts that *Lam. longicruris* De la Pyl. should continue to be separated from the other two species. However, having studied the majority of specimens identified by L. K. Rosenvinge as *Lam. groenlandica*, the only differences I have yet found between this species and *Lam. cuneifolia* are variations in the length of the stipe and the angle of the base of the blade, and there is considerable overlap in these characters between the two species. The validity of using such characters as stipe length and the shape of the blade for separation of these very similar species is open to considerable question. It is evident to me, both from field experience and herbarium studies, that the shape of these plants is highly variable and seems to be quite responsive to environmental influences. Still, until I have completed

¹ Rosenvinge (1893, p. 849) also claims an understanding of Kützing's specimens when he states after *Lam. cuneifolia* J. G. Agardh, "non *Lam. cuneifolia* Kützing, *Phy. Gen.*, p. 345."



●=verified records, ○=unverified records.

Fig. 5. Distribution of *Laminaria cuneifolia* J. G. Agardh.

further field studies on these particular species I hesitate to unite them. Until that time also I must defer the changing of the name of *Lam. cuneifolia*, for if these two species prove to be indistinct, as I suspect, then *Lam. groenlandica* should be the synonym chosen to replace Agardh's illegitimate name.

Distribution: *Laminaria cuneifolia* is recorded only from arctic and subarctic environments. Perhaps further investigations will reveal an abundant circum-polar distribution. Now, however, it is accurately known from a relatively few localities.

Ruprecht, F. J. 1851. *Lam. saccharina* var. *latifolia*, Schantar Islands, southwestern Mare Ockotsh.

- Dickie, G. 1852. *Lam. saccharina*, west side of Baffin Bay and Barrow Strait.
Agardh, J. G. 1872. *Lam. cuneifolia*, Jakobshavn, west Greenland.
Rosenvinge, L. K. 1893. *Lam. cuneifolia*, Jakobshavn to Upernivik west Greenland.
Taylor, W. R. 1957. *Lam. cuneifolia*, northern Labrador and northeastern Ungava Bay, Quebec.
Wilce, R. T. 1959. *Lam. cuneifolia*, northern Labrador and northeastern Ungava Bay, Quebec.

Unverified records:

- Postels and Ruprecht 1840. *Lam. saccharina* forma *cuneata*, northwest North America. No specimen available for study.
Gobi, C. 1874. *Lam. cuneifolia*, Solowetzki Islands, southern White Sea. Extremely doubtful because of the boreal nature of the vegetation of this sea.
Ashmead, A. 1864. *Lam. saccharina*, Floeberg Beach, west coast of Smith Sound.
Dickie, G. 1866. *Lam. saccharina*, Baffin Island, Cumberland Sound.
Sinova, E. C. 1928. *Lam. cuneifolia*, Kamtschatka. No specimen available for study.

Incorrect records:

- Dickie, G. 1880. *Lam. caparata*, Baffin Island, Cumberland Sound.
Kjellman, F. R. 1883. *Lam. cuneifolia*, Siberian Sea (Irkaypi, Koljutshin Isle and Pitlekay).
Saunders, De A. 1901. *Lam. cuneifolia*, Popof Island, northwest Pacific, One of the Shumagin group.
Setchell and Gardner 1903, 1912, 1925. *Lam. cuneifolia*, St. Lawrence Island, Alaska to Puget Sound, Washington.
Zinova, A. D. 1955. *Lam. cuneifolia*, Wrangell Island.

Summary

1. The investigation of *Lam. cuneifolia* J. G. Agardh was begun after the author's discovery of the earlier publication of *Lam. cuneifolia* Kützinger.

2. All of the available syntype of *Lam. cuneifolia* J. G. Agardh were carefully examined and found to include one collection of *Lam. saccharina* (L.) Lamourx., which differs anatomically from *Lam. cuneifolia*. The only other collection representing syntypes proved to agree in all respects with the description and remain as *Lam. cuneifolia* J. G. Agardh.

3. Two annotated but uncited specimens were found in Agardh's herbarium. One is referable to *Lam. saccharina*; the other, the "Esquimalt" specimen, is neither *Lam. saccharina* nor *Lam. cuneifolia*.

4. The "Esquimalt" specimen can be distinguished from *Lam. saccharina* by the presence of mucilage canals in the stipe. It can be distinguished from both *Lam. saccharina* and *Lam. cuneifolia* by its dark color, coriaceous texture, and by the size, shape and arrangement of its surface cells and their protoplasts.

5. The North American west coast plants described by Setchell and Gardner as *Lam. cuneifolia* f. *subsimplex* agree in all respects with the "Esquimalt"

specimen, which was apparently assumed by these authors to represent Agardh's species. However, these plants must be considered, along with the "Esquimalt" specimen as distinct from *Lam. cuneifolia* J. G. Agardh.

6. The misinterpretation of *Lam. cuneifolia* has led to some confusion in the distribution records and the establishment of the general range of Agardh's species, which in reality is strictly a cold-water species.

7. The problem of the identity of these American west coast plants of the "Esquimalt" type and their possible relationship to the other digitate species of *Laminaria* with mucilage canals in the stipe and blade is reserved for further study.

8. Although Agardh's *Lam. cuneifolia* has been shown to be rather easily defined by its ensemble of characters and by its extreme northern distribution, there is considerable question whether it is distinct from *Lam. groenlandica* Rosenv. Kützing's *Lam. cuneifolia* is a synonym of *Lam. saccharina* (L.) Lamourx. and thus cannot be used for Agardh's species. The choice of a name to replace *Lam. cuneifolia* J. G. Agardh must be deferred until further studies can be made on *Lam. groenlandica*, a possible synonym of the former species.

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Six Notes on Pollen Morphology and Pollenmorphological Techniques

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On the swelling of pollen grains in glycerine jelly [J.R.P.]

In palynology the establishment and maintenance of sporothekes, i.e. collections of reference slides of pollen grains and spores, is of great importance. Glycerine jelly, already introduced in microscopical techniques a century ago, is still often used as an embedding medium in the preparation of the slides. Its chief drawback is the fact that pollen grains and spores embedded in it are liable to swell.

In order to study the approximate amount of swelling eight pollen grains of hazel and aspen in test slides made three years ago have been remeasured from time to time [Leitz eyepiece $\times 10$ (Trommelokular), fluorite immersion objective $\times 95$, num. ap. 1.32]. Glycerine jelly according to Kisser's recipe (Zeitschr. wiss. Mikroskopie, Vol. 51, 1935) was used as the embedding medium. The slides were sealed with paraffine (melting point 72 centigrades) under the cover slip. The results are collocated in Tab. I and II.

The tenui-exinous pollen grains in *Populus tremula* show a lesser degree of swelling than the more thickwalled hazel pollen grains. Grains that have been chlorinated after acetolysis swell slightly more than those which have been subjected to acetolysis only.

Some of the slides in the sporotheke of the Palynological Laboratory which were made 26 years ago are still in a perfect condition. Several slides have, however, deteriorated over the lapse of years chiefly because of the use of glycerine jelly with a higher water content than jelly made according to Kisser's formula, or from inadequate sealing. During the past few years efforts have been made to concentrate, in

Table I. *Corylus avellana* (fresh pollen grains)
Diameter in μ

Date		Acetolyzed				Acetolyzed and chlorinated			
		Grain 1		Grain 2		Grain 3		Grain 4	
		Dia- meter	Increase	Dia- meter	Increase	Dia- meter	Increase	Dia- meter	Increase
April	1956	30.94		31.07		33.66		33.32	
July	1956	31.28	0.34	31.21	0.14	34.06	0.40	33.80	0.48
December	1956	31.62	0.34	31.72	0.51	34.51	0.45	34.10	0.30
July	1957	31.68	0.06	31.82	0.10	34.91	0.40	34.10	0.07
January	1958	31.79	0.11	32.17	0.35	34.98	0.07	34.34	0.17
July	1958	31.96	0.17	32.17	0.00	35.02	0.04	34.40	0.06
April	1959	31.96	0.00	32.40	0.23	35.30	0.28	34.70	0.30
Total increase			1.02 μ		1.33 μ		1.64 μ		1.38 μ

Table II. *Populus tremula* (fresh pollen grains)
Diameter in μ

Date		Acetolyzed				Acetolyzed and chlorinated			
		Grain 5		Grain 6		Grain 7		Grain 8	
		Dia- meter	Increase	Dia- meter	Increase	Dia- meter	Increase	Dia- meter	Increase
April	1956	32.36		33.83		30.60		32.02	
July	1956	32.36	0.00	34.00	0.17	30.73	0.13	32.40	0.38
December	1956	32.47	0.11	34.00	0.00	30.94	0.21	33.05	0.65
July	1957	32.47	0.11	34.14	0.14	31.07	0.13	33.30	0.25
January	1958	32.50	0.03	34.34	0.20	31.58	0.51	33.30	0.00
July	1958	32.54	0.04	34.34	0.00	31.64	0.06	33.32	0.02
April	1959	32.58	0.04	34.82	0.48	31.68	0.04	33.32	0.00
Total increase			0.22 μ		0.99 μ		1.08 μ		1.30 μ

each slide, a large amount of pure or almost pure pollen or spore material in a small circular area (diameter about 1—4 mm) under the centre of the cover slip.

On spinuloid processes in pollen grains of the Betulaceae and Juglandaceae [G.E.]

By means of electron microscope investigations (enlargement 1200—8000 times) of exine surfaces, based on the carbon replica method, Yamazaki and Takeoka ("Electronmicroscope investigations on the surface structure of the pollen membrane, I, II", Journ. Jap. Forestry Soc., Vols. 39, 40, 1957, 1958) have been able to demonstrate the presence of

minute spinuloid processes, i.e., in pollen grains of *Alnus sieboldiana*, *Carpinus carpinoides*, and *Juglans sieboldiana*. As shown in Pl. I (*Alnus glutinosa* and *A. incana*), Pl. II (*Betula pubescens*, *B. verrucosa*, *B. nana*, and *Carpinus betulus*), and Pl. III (*Juglans regia*) the occurrence of what seems to be spinuloid processes can also be traced, although in a less distinct way, in ordinary photomicrographs.

In *Alnus glutinosa* (Pl. I, Fig. a) the spinuloid elements appear as dark, more or less irregular patches at the centre of the figure. At slightly higher focus they appear bright against a greyish background (cf. the lower left-hand part of the central area of the figure). They can also be seen in Figs. c and d, as well as in a swollen grain (Fig. e) from an old slide. Because of the presence of spinules the lower left-hand contour of the last grain is not quite smooth. With phase contrast distinct spinules can be seen in thin sections (thickness about 0.5 μ).

The presence of spinuloid elements in *Alnus incana* is indicated in Pl. I, Fig. g, in *Betula* and *Carpinus* in Pl. II, Figs. a, c, d, f, and h. Attention should be drawn to the potential value of using fine morphological characters, such as spinuloid processes, aperture details and exine stratification etc. for specific determinations in recent as well as in fossil (Quaternary) pollen grains.

The exine surface in *Juglans regia* is slightly scabrate, provided with small, densely and regularly spaced spinuloid processes (Pl. III), bright at high, dark at low focus. The apertures are operculate. Two opercula shown in Pl. III, Fig. b, are bright (high focus), two others greyish (lower focus; cf. also Pl. III, Fig. c).

As shown, e.g. in several papers published during the past ten years by Dr. I. Cookson, Melbourne, the pollen grains in *Nothofagus* possess small spinules or spinuloid processes readily discernible under an ordinary microscope. This is true of recent as well as of fossil, Quaternary to Cretaceous grains. The spinules may possibly form a sort of counterpart to the minute spinuloid processes in *Alnus*, *Juglans* etc.

Further investigations are necessary in order to decide whether the occurrence of spinuloid processes can be used as a character for distinguishing — particularly in palaeobotanical research — pollen grains of plants of the "Amentiferae" group from grains of other plants. The same applies to the importance of the aperture type in the same group. The apertures (Gr. trema, plur. tremata) are often "diplotrete", i.e. they consist of two perforations, one in the outer layer of the exine (the sexine) underlain by another perforation in the inner layer (the nexine). Usually these perforations are not congruent as seen, e.g., in Pl. I, Figs. c

and d (the sexinous part of the aperture in *Alnus glutinosa* is generally a colpus, i.e., the long axis is more than twice as long as the short axis; the inner, nexinous part — cf. Fig. d — is almost as broad as it is long). In *Juglans* and *Carya* etc. the size difference between the outer and the inner part of the apertures is still more striking.

Photomicrographs of the exine surface in grass pollen grains (cereals) [G.E.]

Attention has previously been drawn to some ways of increasing the possibilities to make generic or specific etc. determinations of grass pollen grains: cf. e.g. "Pollen morphology of the cereals. With notes on the pollen morphology in *Triticale*", Svensk bot. Tidskr., Vol. 38, 1944 (in Swedish, with summary in English), and "Current trends in palynological research work", Grana Palynologica, N.S., Vol. 1: 2, 1956.

In the latter paper there are some phase contrast photomicrographs (Fig. 3, a—c, p. 135) of the exine surface in some grass pollen grains, and it is argued that phase contrast microscopy facilitates "the possibility of determining even the cereal species by means of fossil as well as recent pollen grains". A preliminary note on this subject was published in a Swedish newspaper in April 1955. Dr. Udelgardh Grohne, Wilhelmshaven, when visiting the Palynological Laboratory in August 1955, mentioned that she also had used phase contrast microscopy in the same context. She has recently published an interesting paper on the subject ("Die Bedeutung des Phasenkontrastverfahrens für die Pollenanalyse, dargelegt am Beispiel der Gramineenpollen vom Getreidetyp", Photographie und Forschung, Bd. 7, December 1957).

Pl. IV provides two pictures of the exine surface in *Triticum aestivum*: the upper (a) is a phase contrast picture, the lower (b) an ordinary photomicrograph. Pl. V shows, in phase contrast, the exine surface in *Hordeum vulgare* (a) and *Avena sativa* (b). The figures are all reproduced in the same scale, $\times 4800$ (4×1200). The phase contrast pictures provide information of both suprategillar coarser elements and of infrategillar baculoid rods.

On the pollen grains in *Hedychium coronarium* [G.E.]

In the pollen walls of *Heliconia aurantiaca* a thick layer with a faint radial structure and not resistant to acetolysis has been described (Pollen Morphology and Plant Taxonomy, I. Angiosperms, 1952; cf. Fig.

160 B, p. 276). As shown in Pl. VI a layer more or less similar to the so far unique layer in *Heliconia*, occurs in *Hedychium coronarium* (Zingiberaceae; material from Tijuca, Brazil, coll. G. Erdtman, Dec. 1958). The layer is difficult to see by means of an ordinary microscope (cf. Fig. 5, Pl. 41, in M. Ikuse, Pollen grains of Japan. Tokyo 1956). In UV micrographs of thin sections sundry details can, however, be revealed.

As seen in the left part of the plate the radially structured (baculate?) layer is severed from the cytoplasm by a layer (intine?) which seems susceptible to swelling. Empty space (about 1—2 μ m long in the plate) are seen in three places at the inner border with the radially structured layer. The irregular, highly refractile particles at the sporoderm surface are not, as was first believed, remains of the embedding medium. They may more likely represent an acetolysis-proof (exinous) part of the sporoderm. (After acetolysis this part usually comes out in a very shrivelled state).

Further description is deferred since the aim of these lines is merely to furnish an example of the use of UV microscopy in the investigation of pollen grains and spores.

On aperture membranes etc. in the pollen grains of some proteaceous plants [G.E.]

Ten years ago Dr. I. Cookson and the present author worked together in an attempt to classify the sporoderm layers in the Proteaceae. Special attention was paid to the aperture membranes which are frequently quite conspicuous in this family. We soon realized, however, that morphogenetic studies were necessary to provide a satisfactory approach to the solution of the intricate problems involved. Preliminary results of our investigations were published in "Pollen Morphology and Plant Taxonomy. I. Angiosperms", Stockholm 1952, pp. 339—369.

A reinvestigation of some of the pollen types has, i.e., led to the following deductions. The aperture membranes in mature grains of *Hakea laurina* (Fig. 1 d) consist of two layers. The outer layer, dotted in the illustration, is thicker and less refractile than the inner layer (x). The aperture membrane is underlain by a layer of thickened intine (in). In younger pollen grains the pre-stages of the outer layer of the aperture membranes have the shape of large plugs, the bases of which are wedged in within the nexinous brim of the apertures and delimited towards the interior of the grains by a highly refractile layer. The apertural parts of the latter are confined within the "infraexinous" part of the

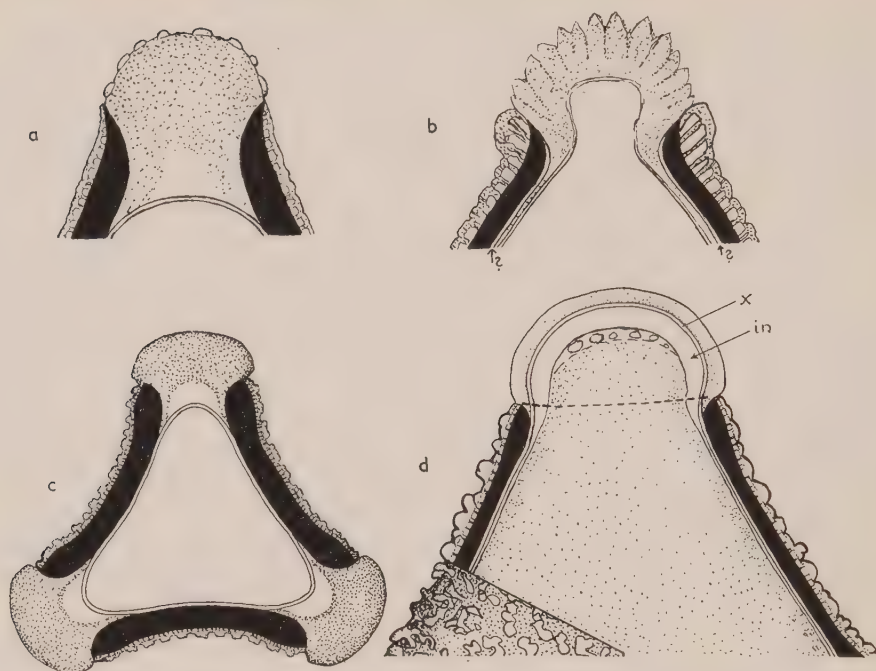


Fig. 1. Proteaceae, sporoderm stratification. — a, *Hakea ceratophylla*, aperture, optical cross-section (about $\times 800$). — b, *H. glabella*, aperture, optical cross-section (about $\times 800$). — c, *H. laurina*, young pollen grain in polar view; optical cross-section ($\times 350$). — d, *H. laurina*, part of palynogram of mature pollen grain in polar view. Lower left-hand part: surface; rest of figure: optical cross-section ($\times 800$).

grains (Fig. 1 c). During the development of the pollen grains they protrude and eventually form the inner layer (x) of the aperture membranes (Fig. 1 d).

With a view, i.e., to the recent findings of Ehrlich [Exptl. Cell Res. 15 (3), 463 (1958)] and Ehrlich and Hall [Grana Palynologica 2 (1), 32 (1959); cf. also Hall, *ibid.*, 2 (1), p. 20 (1959)], as well as to my own observations on the aperture membranes in *Agrostemma*, *Cyrtanthera*, and *Knautia* etc., it would seem justified to suspect that this layer is endonexine or “mesine” as suggested by Hall l.c. (in spite of the fact that Fitting, in another sense, has used the term mesosporium; if shortened, mesosporium would read mesine; cf. perisporium—perine, etc.). Endonexine was described by the present author in 1948, but it has generally not been recognized by other workers.

It may also, tentatively, be suggested that the outer layer of the aper-

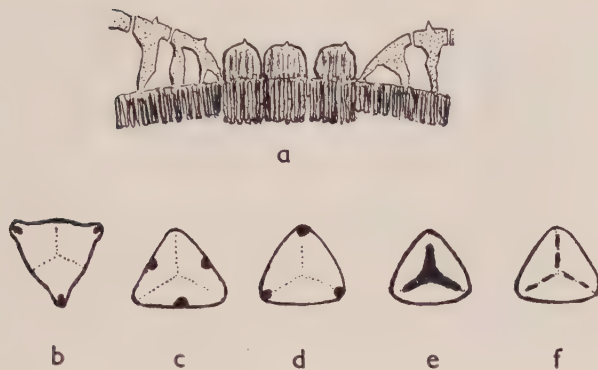


Fig. 2. — a, *Alluaudiopsis fiherensis* Humbert et Choux (Didiereaceae), exine stratification (about $\times 850$). — b—f, radiosymmetric pollen grains and spores in polar view (diagrams; distal pole facing the observer). Apertures marked by large black dots in b—d, by a three-lobed black area in e, and by a three-lobed marking (broken lines) in f. The fine dotted lines denote the contact lines (as seen in this particular projection) between the three remaining members of a supposed tetrad. — b, *Betula*-type. — c, *Ceiba*-type. — d, *Proteaceae*-type. — e, *Elaeis*-type. — f, *Selaginella*-type.

ture membranes (i.e. the layer formed by the plugs) is an outer, modified layer of the endonexine. In pollen grains of *Hakea glabella* (Fig. 1 b) the plugs possibly result from a local hyperplastic growth of an extremely thin sporodermal layer intercalated between the main part of the exine and the strongly refractile (part of) the supposed endonexine. In *Hakea ceratophylla* (Fig. 1 a) the distal surface of the plugs is studded with small, distinctly delimited refractile granules, which, from their appearance, could be of a sexinous nature.

In Fig. 2 b—f are shown the apertures and main outlines of five triangular or subtriangular radiosymmetric pollen grain and spore types in polar view (distal face up). The fine dotted lines denote the contact lines (as seen in this particular projection) between the three remaining members of a supposed tetrad. It can also be said that they would coincide with a "tetrad scar" if such a scar be present. In the *Proteaceae* type (Fig. 2 d) the apertures are situated in the corners that would be reached by the arms of a tetrad scar or by their extensions. In this respect the *Proteaceae* differ from the great majority of the angiosperms (cf. the *Betula*-type, Fig. 2 b, and the *Ceiba*-type, Fig. 2 c).

In *Elaeis guineensis*, as found in grains still united in tetrads (material kindly supplied by the West African Institute for Oil Palm Research,

Benin City, Nigeria) the aperture arms are extended towards the corners corresponding — with regard to the arrangement of the tetrads — to the aperturiferous corners in the Proteaceae (Fig. 2 e; cf. also the *Selaginella* type, Fig. 2 f, which is provided with a tetrad scar, indicated by heavy broken lines, in the proximal spore face).

To the above lines on aperture membranes and aperture arrangement in the Proteaceae may be added that fine, more or less perpendicular channels (tubuli) in the nexine occur in *Synaphaea* and in *Hakea prostrata*. In the Proteaceae tubuli have previously been reported only from *Conospermum*.

This affords a memento with regard to the possibilities of tracing, by means of ordinary microscopy, certain small details of the nexine (endexine), which layer has hitherto generally been held to be more or less homogeneous, without much morphological interest. Another, and more striking, hint in the same direction was provided from a reinvestigation of the pollen grains of a rare didiereaceous species from Madagascar, *Alluaudiopsis fiherensis* Humbert et Choux; Humbert 11588, Herb. Mus. Paris. Fig. 2 a shows an outline of an optical cross-section through an aperture, a colpus, in a pollen grain from this specimen. The nexine of the colpus membrane is thicker than that of the adjoining mesocolpia. The sexine of the latter is tectate, provided with a punctate, spinuliferous tegillum supported by sturdy bacula. In contradistinction, the sexine of the colpi is intectate, composed of cubical bodies about 4 μ high, often provided with a spinuloid process. There is reason to believe that these "cubes" are formed by closely packed, more or less amalgamated baculoid elements. The same, beyond any doubt whatsoever, is the case with the nexine, particularly the apertural part of it. Its densely packed, perpendicular baculoid elements are easily discernible in an LO-analysis. This feature can have been overlooked at the examination ten years ago. Another explanation might be that in the lapse of years the nexine has swelled so as to make it possible to detect, without difficulty, the baculoid components. Be that as it may, an occurrence of baculoid elements in the nexine, of infra- and intrategillar bacula (columellae), of suprategillar bacula, and of transitions and combinations between various baculoid elements seems to provide another argument for a terminological unification, viz. the use of the term bacula (or baculoid elements) as an overall term for rodlike, more or less perpendicular sporodermal elements. This does not, of course, preclude the use of the term columellae for a special kind of rods.

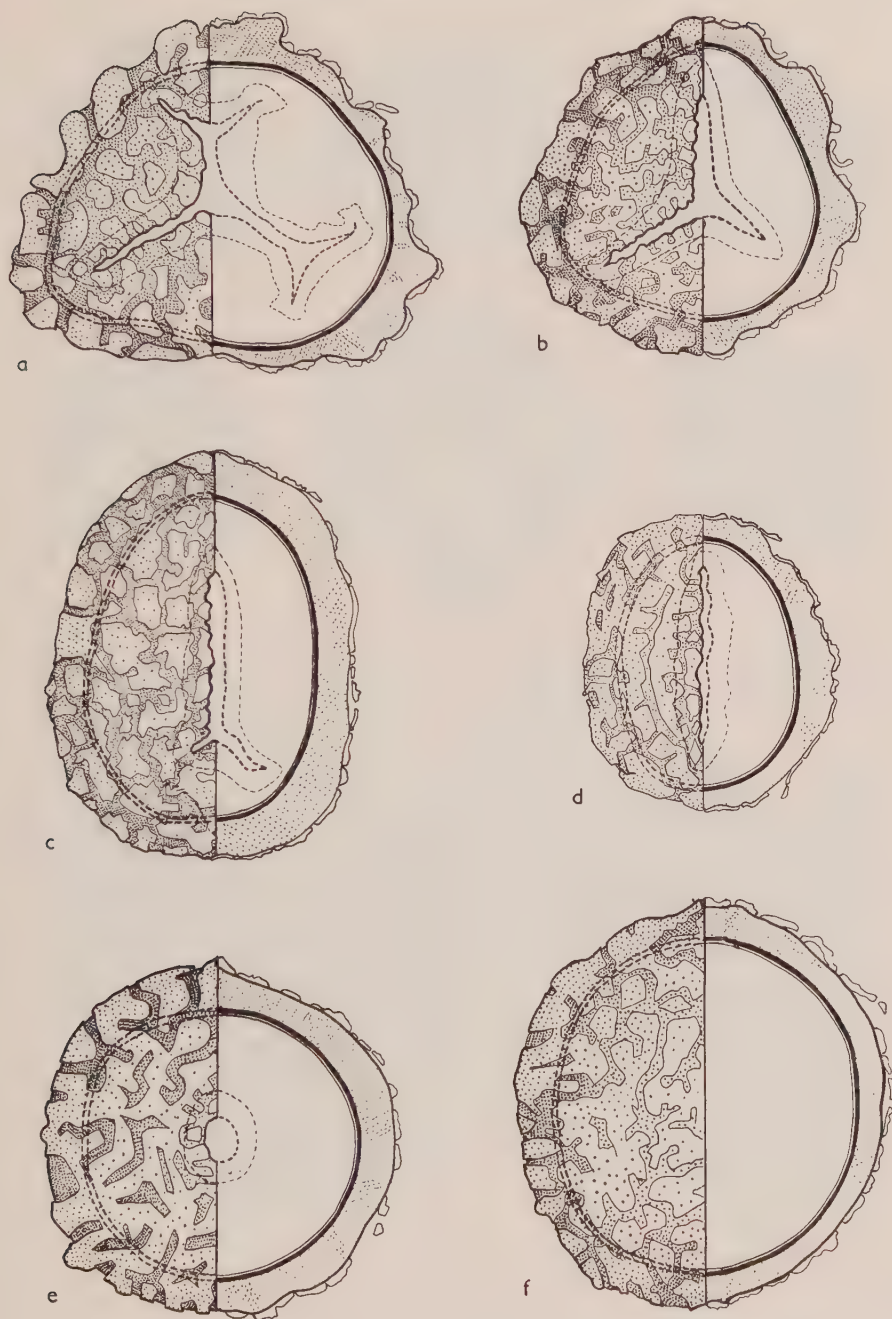


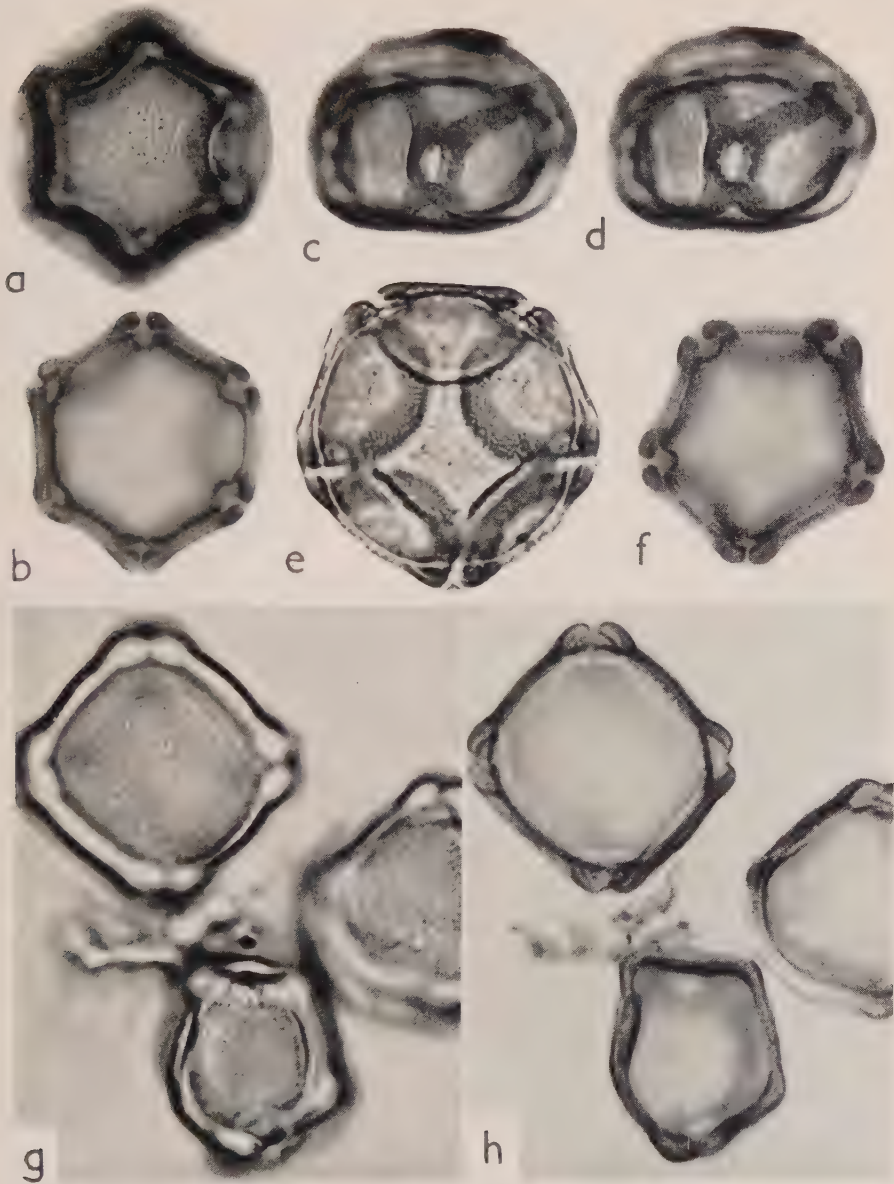
Fig. 3 a—f, *Pityrogramma hybrida* var. *maxima*, spores. The outermost layer in the optical sections on the right side of each figure consists of perine fragments. As shown on the left side of the figures the perine forms an irregular reticulum or mere fragments of a net. $\times 500$.

On the spores in "*Pityrogramma hybrida* var. *maxima*"
(*P. calomelanos* × *chrysophylla*). [J.R.P.]

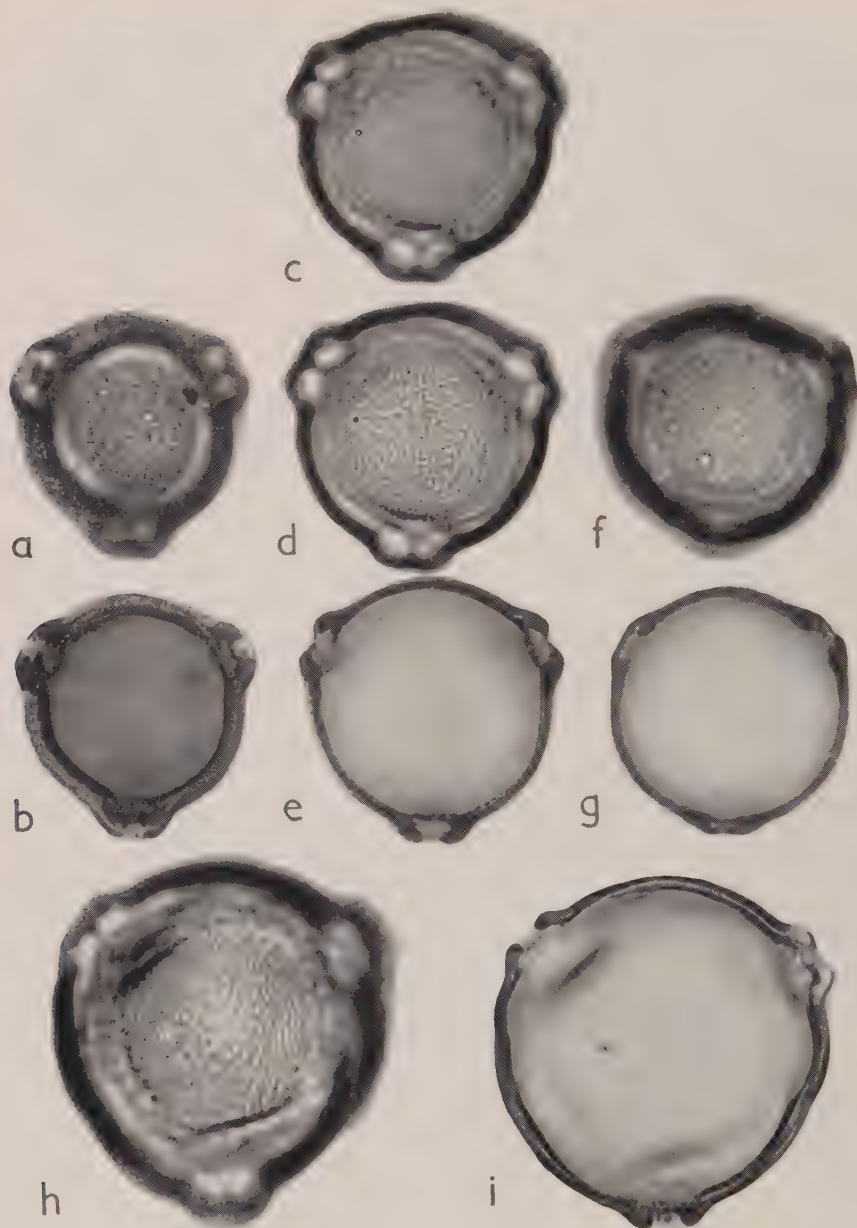
The material investigated comes from specimens cultivated at the Royal Botanic Gardens, Kew. Normal *Pityrogramma* spores are trilete (more or less of the same shape as the spore in Fig. 3 b). In the spores of the hybrid there are transitions from comparatively large trilete spores with bifid laesura arms (Fig. 3 a) to trilete spores (3 b) and spores showing a transition from a trilete to a monolete conditions (3 c). A monolete spore is figured in Fig. 3 d, a monoporate (cataporate) spore in Fig. 3 e, an alete spore (without laesura) in Fig. 3 f. Small alete spore-like bodies often stick together, forming more or less irregular globules.

The features mentioned speak — as do similar findings by A. N. Sladkov in *Pteris cretica* (Dokl. Akad. Nauk USSR, vol. 117, pp. 900—903, 1957) — in favour of the apertural status in pollen grains and spores being less dependent on haptotypic factors than hitherto generally believed (cf. also the intraspecific pollenmorphological variation in *Rorippa silvestris* as well as the pollen morphology in the hybrid *Betula nana* × *tortuosa* described by Erdtman in Flora, Vol. 146, 1958, pp. 408—411).

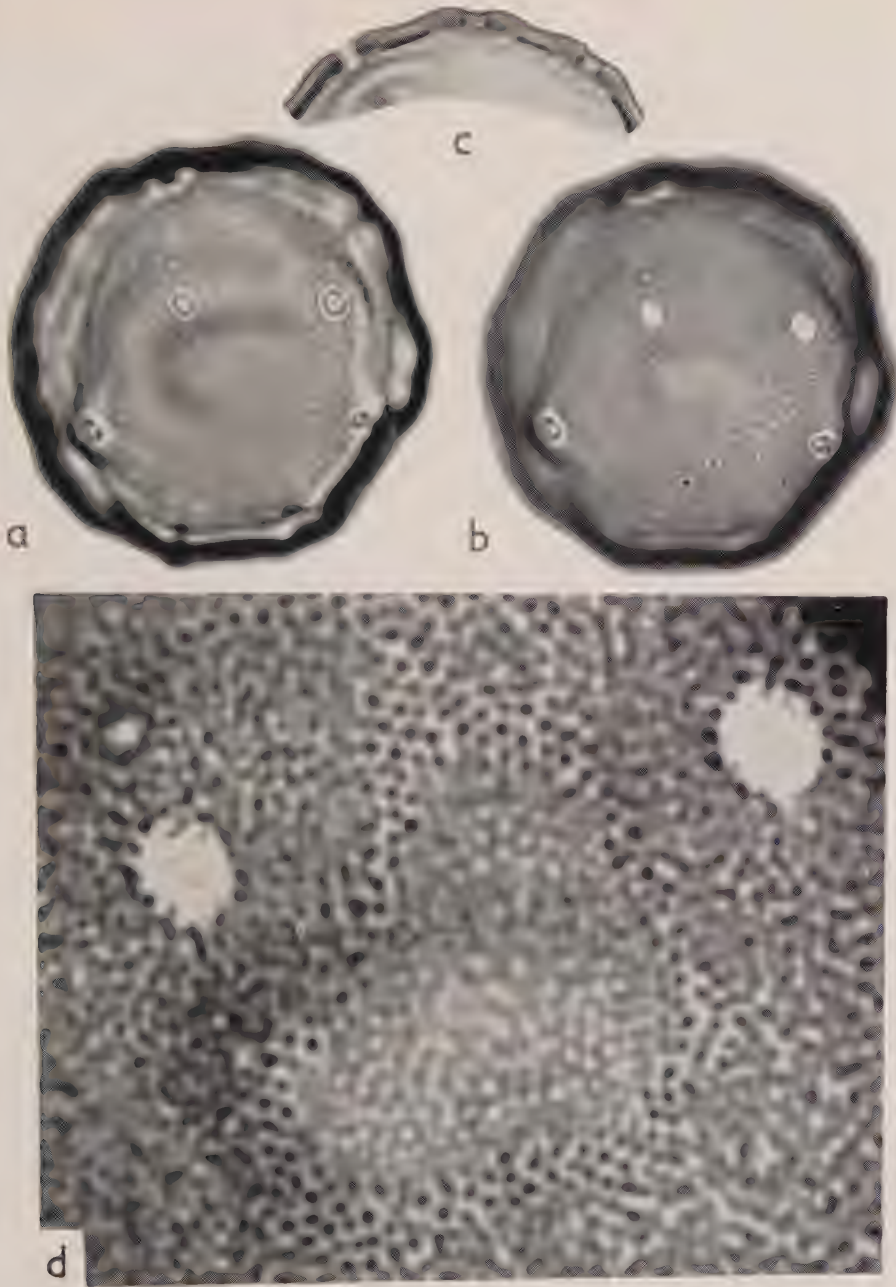
For technical reasons it has not been possible to reproduce most of the illustrations in the usual series of magnifications (×500, 1000, 2000, 4000). The orientation of the pollen grains in Figs. 1—3 and Pl. I and II is in accordance with the suggestions in "Pollen Morphology and Plant Taxonomy. I" (p. 17) recently re-emphasized by the senior author in "Some remarks on pollen and spore illustrations" (Pollens et Spores, Vol. I: 1, Paris 1959).



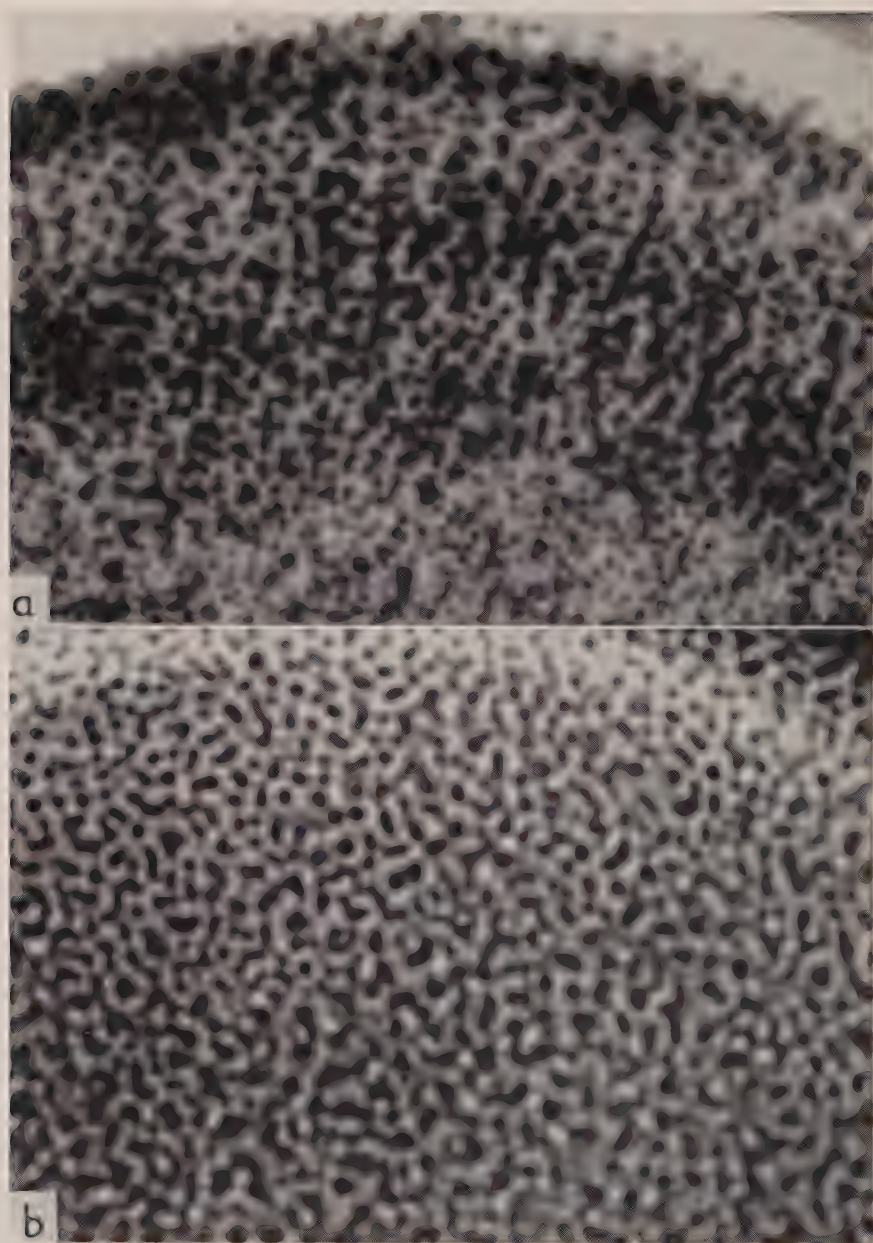
PL. I. *Alnus*, acetolyzed fresh pollen grains. a—f, *A. glutinosa*, g—h, *A. incana*. — a, hexatreme grain, polar view. — b, same grain, optical cross-section. — c, d, pollen grains in lateral view with an aperture at high (c) and low (d) focus. — e, swollen, pentatreme grain, polar view. — f, pentatreme grain, optical cross-section. — g, h, pollen grains at high (g) and low (h) focus. $\times 1200$ K. E. Samuelsson photo.



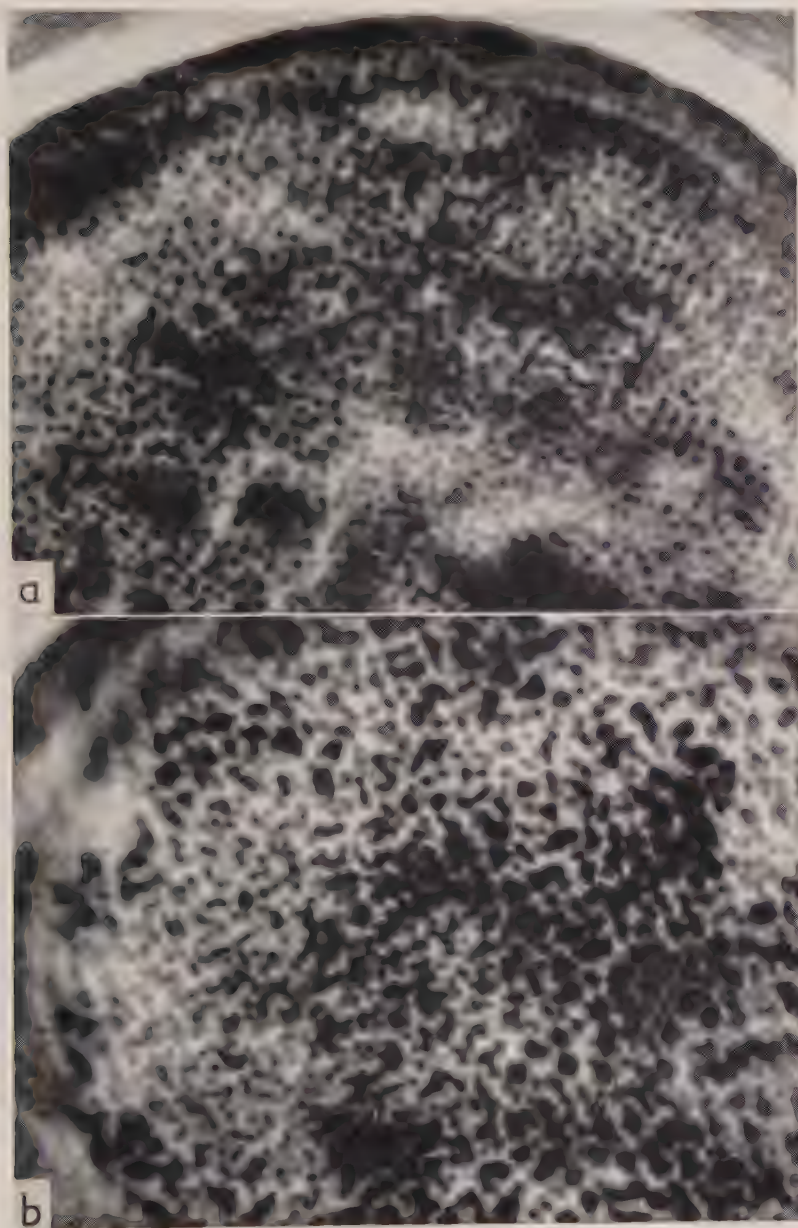
Pl. II. Acetolyzed fresh pollen grains of *Betula* (a—g) and *Carpinus betulus* (h, i). — a, b, *Betula pubescens* (medium, and low focus). — c—e, *B. verrucosa* (high, medium, and low focus). — f, g, *B. nana*. $\times 1200$ K. E. Samuelsson photo.



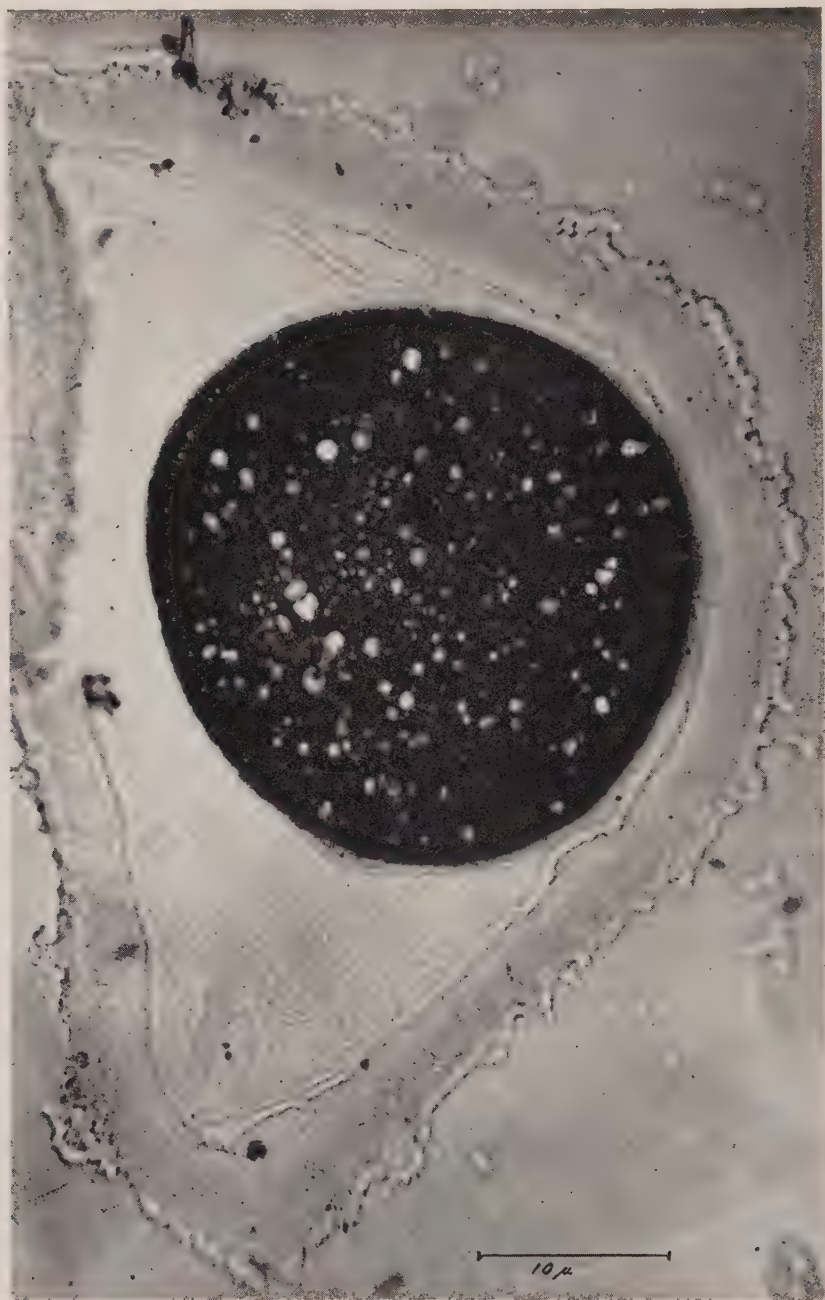
Pl. III. Acetolyzed pollen grains of *Juglans regia*. — a, high focus. — b, low focus. — c, part of exine, optical section (a—c $\times 1200$). — d, part of b, enlarged ($\times 4800$).



Pl. IV. *Triticum aestivum*, part of acetolyzed pollen grain. — a, phase contrast. —
b, ordinary photomicrograph. $\times 4800$ K. E. Samuelsson photo.



Pl. V. *Hordeum vulgare* (a) and *Avena sativa* (b), parts of acetolyzed pollen grains.
Phase contrast. $\times 4800$ K. E. Samuelsson photo.



Pl. VI. *Hedychium coronarium*, section (about $0.5\ \mu$ thick) through a fresh pollen grain preserved in glacial acetic acid. UV micrograph (mercury low pressure lamp, $2536\ \text{\AA}$). $\times 2500$ H. D. Goldmann micr.

Evidence and Interpretation of "Landnam" in the North-East of Ireland

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Introduction

During the past fifteen years palynological work in north-west Europe has been influenced by Iversen's studies on the "landnam" or literally "land-take" phenomenon in Denmark. The first of his studies appeared in 1941 and in the succeeding years his ideas on this topic became rapidly more and more familiar to British workers who have, of course, tried to discover similar or comparable effects of the Neolithic occupation on the woodlands of the British Isles. Godwin (1944 A, 1944 B, 1948) provided the first clear evidence from England, while Mitchell (1951, 1956) has found plentiful evidence in many of the Irish raised bogs. The object of this paper is to present some new data on "landnam" from the north-east of Ireland and to consider how a close analysis of these facts affects our ideas on the composition and structure of the Irish deciduous woodland of the Atlantic and Sub-Boreal periods. Two sites have been examined closely and the evidence from both is similar. The subsequent account is concerned with only one site, namely Parkmore, which lies on the basaltic plateau of the north-east of Ireland, (Fig. 1).

The basaltic plateau in question was formed by successive, widespread sheets of lava which overwhelmed the north-east of Ireland during the Tertiary era. These sheets consolidated leaving behind an extensive plateau which is now between 1000 and 1500 feet in height. Much of the area is now moorland with occasional small lakes and vast, desolate stretches of deep and in some places very wet blanket bog. Two sedges not occurring elsewhere in Ireland are occasional over this region, namely *Carex pauciflora* and *C. paupercula*. *Saxifraga hirculus* is also known (Kertland, 1956) and a colony of *Cladium mariscus*, extinct over the remaining north-east of Ireland, was recently identified (Harrison,



Fig. 1. Part of the basaltic plateau of the north-east of Ireland showing principally Glenariff. Parkmore is arrowed. Tievebullagh is an important Neolithic site where stone-axes were made from a rare material-porcellanite.

1956). The seaward edge of the plateau falls away steeply and in some places cliffs afford protection for some of the rarer plants. This seaward margin is also broken and varied by massive land-slips and by narrow, steep-sided valleys — the Antrim Glens — which extend inland for several miles. There are five principal glens radiating into the plateau. In sequence from south to north they are Glenarm, Carnlough, Glenariff, Glenballeymon, and Glendun.

Parkmore, the site of the present study, lies towards the seaward rim of the plateau and at an elevation of 900 feet. It is just slightly above and beyond the head of Glenariff (Fig. 1). It is a large, basin-shaped area which forms the watershed between the Glenravel and Inver rivers. Towards the middle of this great depression — which is entirely blanketed in peat — there is a small round lake, with two shallow in-filled hollows nearby; these indicate former lakelets that have been entirely colonised. The smallest of these hollows — only some thirty metres in diameter — lies alongside the present lakelet, while the other is several hundred metres distant, and 200 metres in diameter.

The deposits in each hollow have been investigated and the strati-

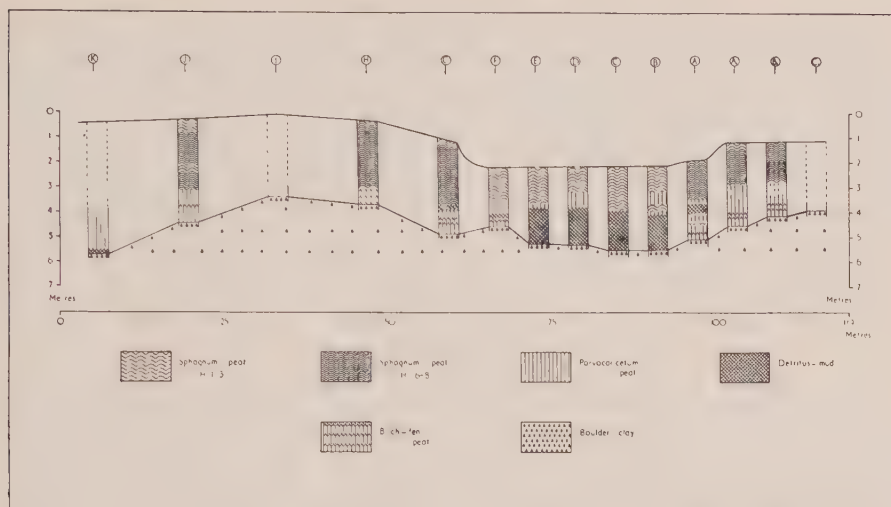


Fig. 2. Parkmore: section of the deposits in the smaller of the two infilled lake-basins.

graphy recorded along levelled transects. In both cases highly humified detritus muds are overlain by loose, spongy *Sphagnum*-peats. The mud in the small hollow is of early Post-glacial age but that in the larger hollow dates back to the Late-glacial period. At the present time this is the highest altitude at which a Late-glacial deposit has been discovered in the north-east of Ireland. The samples for the pollen diagrams were taken at Point J (Fig. 2) in the blanket bog just beyond the smallest hollow. The lake deposits were unsuited for precise sampling because of the upper, loose *Sphagnum*-peat. The stratigraphy was as follows:

- 0—50 cm. Reddish-brown, fibrous *Eriophorum* peat; H. 6.
- 50—180 cm. Reddish-brown, slightly less fibrous peat. Occasional fragments of *Calluna*; H. 8.
- 180—200 cm. Reddish-brown, fairly coarse *Sphagnum*-peat, with still occasional fragments of *Calluna*; H. 4—5.
- 200—286 cm. Highly humified, dark-brown *Sphagnum*-peat; H. 7—8.
- 286—350 cm. Still highly humified peat and now with traces of reed-swamp detritus.
- 350—400 cm. Distinct reed-swamp peat with frequent fragments of wood, cf. *Betula*; H. 8.
- 400—417 cm. Reedswamp peat passing downwards into grey glacial clay. Drill stopped by rock.

One of the strongest factors determining the choice of the Parkmore area for study was its topographic uniformity. Around the point where the sampling was made there is a large area of relatively flat ground now, of course, peat covered. At a greater distance the ground falls away gradually into the great glen or slopes smoothly upwards to the surrounding hills. There is nothing which would have created aberrant or atypical features in the former woodland which must have covered the area. Here and there cuttings in the bog reveal pine stumps.

Methods

The samples were taken at 5 cm., intervals using a Hiller sampler. They were prepared for microscopic examination as described by Faegri and Iversen (1950). Throughout, the pollen was plentiful and in an excellent state of preservation. For each sample never less than 1000 tree-pollen, including *Corylus*, were counted.

The construction of the pollen diagrams follows the plan adopted by Iversen (1941, 1949) for investigating "landnam". *Corylus* is included in the Basic Sum from which the pollen percentages are derived. Prior to its inclusion, however, its pollen count is divided by four, and likewise the values for *Betula*, *Pinus*, and *Alnus*. These genera all produce pollen in much greater abundance than *Quercus*, *Ulmus*, and *Fraxinus*, so that the quartering of the counts is an attempt to eliminate the inequality of the pollen production. The theoretical basis of this procedure is discussed by Faegri and Iversen (1950), and seems to receive considerable support from Jonassen's (1950) work on recent pollen sedimentation in Jutland. In all the pollen diagrams the non-tree pollen (NTP) percentages have been calculated using a Basic Sum comprising only the NTP and not — as is usual — the total tree-pollen (TP).

Zonation of the pollen diagrams

The zonation of the pollen diagrams is according to the scheme recently recommended by Mitchell (1956) in his important paper "Post-Boreal pollen diagrams from Irish raised bogs". The previous system for Irish diagrams involved eight zones, I—VIII, and was based on Jessen's (1949) views, but with slight modifications which had been introduced by Mitchell (1951). Mitchell's new system contains ten zones, I—X, and is to some extent a development of the views outlined in his 1951 paper. The core of Mitchell's argument in support of the new system is best given, perhaps, in his own words:

"Jessen in his 1949 paper drew a confident line between the Sub-Boreal and the Sub-Atlantic periods, though for its position the line rested heavily on a recurrence-surface which was considered not only to be synchronous in those Irish bogs in which it was developed but also to be contemporaneous with the *Grenzhorizont* of Weber and other continental authors . . . In my 1951 paper considerably less confidence was shown, and because of uncertainty the line was omitted from several diagrams. Since 1951 the process of erosion has continued and I can now offer no pollen feature on which to base a line of demarcation between these two periods. Nor can I any longer believe in any absolute contemporaneity of the recurrence-surfaces in Irish raised bogs. Consequently I am compelled to abandon the zonation hitherto adopted for the later stages of Irish pollen diagrams". (Mitchell, 1956.)

Mitchell leaves unmodified Zones I—VI inclusive of the old system. As previously the commencement of Zone VII is associated with the rational border of *Alnus*, though other features are also considered. The close of the zone and the start of Mitchell's new succeeding Pagan Period falls at the first evidence of "landnam" or human interference with the woodlands. This has been dated tentatively to around 3000 B.C. (Mitchell, 1958). The Pagan Period has been formed by fusing together the former Sub-Boreal (VII b) and Sub-Atlantic (VIII) periods. The result is a new, very long zone which becomes Zone VIII. This is split into two sub-zones VIII a and VIII b by the absolute *Quercus* maximum which appears to fall about 1500 B.C. (Mitchell, 1958). In practice these two new sub-zones are almost equivalent to the old Sub-zone VII b and Zone VIII, respectively. However, not all of the former Sub-Atlantic period is fused to the Sub-Boreal since the upper or later part is subtracted to create the two new zones IX and X. Neither of these is of paramount significance. Zone IX — the Christian Period — is often difficult to recognise. Its lower border is defined by the final diminution of *Ulmus*, but usually this is difficult to discover precisely since *Ulmus* frequently has fallen already to very low values at a much earlier date. This is particularly the case in districts with non-calcareous soils. Zone X is referred to by Mitchell as the Afforestation Period, and its opening is indicated by the appearance of pollen of trees commonly planted in Ireland, namely *Pinus* and *Fagus*. Most of these tree-plantings were made by private land-owners during the eighteenth century. *Fagus* appears to have been native in England but did not reach Ireland (Godwin, 1956). *Pinus* on the other hand although an important genus of the early Post-glacial Irish woodlands is believed to have become extinct in Ireland during the course of the Sub-Boreal period. Only in the north of the British Isles, in Scotland, does it appear that *Pinus* survived to the present day.

The Pollen Diagrams

The base of the diagram (Fig. 3) begins late in the Post-glacial period and corresponds to the end of Zone VI, presumably Sub-zone VIc. The *Alnus* curve originates a short distance above the base and continues with low values until it begins from 380 cm., to rise gradually towards a maximum reached at 315 cm. The rational border for *Alnus* is definitely at 380 cm. but this level has not all the characteristics demanded by Mitchell (1951) for the Zone VI/VII transition. However, it is the only place on the present diagram where this transition could reasonably be placed.

Zone VII, with its ascending *Alnus* and falling *Corylus* values, appears to terminate at 320 cm., where a distinct recession of *Ulmus* and the appearance of pollen of *Plantago lanceolata* indicate early prehistoric activity — perhaps Neolithic. Mitchell (1956) places the boundary between Zone VII and Zone VIII where the first evidence of such “landnam” is discovered. In Irish diagrams this is generally indicated by a fall of *Ulmus*, the appearance of *Plantago*, and sometimes a rise of *Corylus*. In the present case reference to Fig. 4 which elaborates this section of Fig. 3 shows that the very first signs of agriculture — or at least human activity — are actually as low as 345 cm., where a few grains of *P. lanceolata*, *P. major*, and *Chenopodiaceae* occur. It is debatable whether the VII/VIII transition should be placed at the first, feebly-marked sign of “landnam” or at the upper, more clearly defined level. Faced with a similar problem in the zonation of the diagrams from Leigh, Co. Tipperary and Agher, Co. Meath, Mitchell (1956) chose the lower level. He argued that the alternative meant having the first evidence of “landnam” lying in the Atlantic period. This would have created difficulties archaeologically since it is usually assumed that this first “landnam” was caused by Neolithic races. It is of course always possible that these first indications of deforestation are not Neolithic in age but perhaps belong to a semi-agricultural phase which preceeded the Neolithic. This brings to mind Troels-Smith’s (1953) interpretation of the primary *Ulmus* decline in Denmark. Iversen attributed that to climate but Troels-Smith has attempted to show that it was the outcome of the semi-agricultural pursuits of the folk of the Ertebølle culture. These folk were farmers to the extent of having cattle which were fed on leaves and young twigs of *Ulmus*.

Without at present implying any analogy to the Danish sequence I prefer to draw the Zone VII/VIII boundary at the second indication of

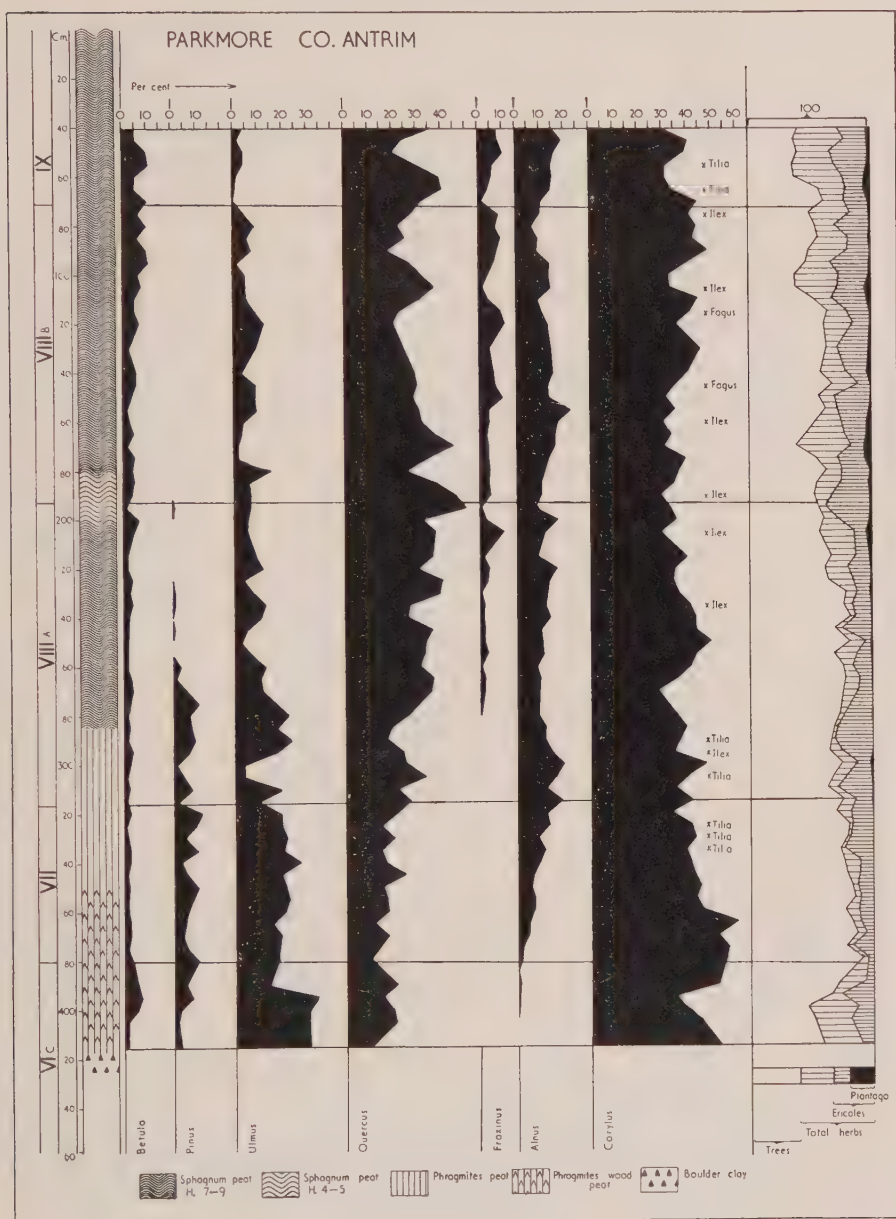


Fig. 3. Parkmore: tree-pollen diagram. Percentages based on total of tree-pollen including *Corylus*. Pollen counts of *Betula*, *Pinus*, *Alnus*, and *Corylus* divided by four before calculations of percentages.

"landnam", that is at 320 cm. Several pollen curves contribute to make this a better defined horizon than the lower at 345 cm. A noticeable feature coinciding with the VII/VIII horizon is the maximum on the *Alnus* curve. This may be nothing more than a very local development. Since, however, an *Alnus* maximum has been observed above the same horizon in a diagram some ten miles westward it may be a feature of some constancy in this area, and should be looked for in further diagrams.

The features of the deforestation phases may now be considered more closely. Fig. 4 allows these to be traced with greater detail than in Figs. 3 and 5. The first sign of activity is at 345 cm., and is indicated by small peaks in the curves for some weeds, but there is no effect on the forest. This is first disturbed noticeably at 315 cm., where there is a small recession of *Ulmus* coinciding with the first distinct *Plantago* peak. A slight recovery of *Ulmus* follows, but then coinciding with a fresh peak of *Plantago* the *Ulmus* falls swiftly to a low value. Undoubtedly this constitutes a well defined clearance and may be designated as the Primary Deforestation. The end of the clearance is marked by the restoration of *Ulmus* to its previous importance. It will later be seen that this complete restoration is perhaps significant.

After the Primary Deforestation the *Ulmus* remains at fairly high values over several samples and the *Plantago* curve vanishes. The area appears to have experienced a respite from Neolithic people for, perhaps, several hundred years. Thus, here as at many other Irish sites which have been examined the Primary Deforestation is distinctly isolated from the subsequent clearances. Since this is a common feature and is widespread it is worth emphasising. Its significance archaeologically can only be vaguely surmised. It seems as though a wave of Neolithic immigrants spread across the countryside and made only temporary settlements which are indicated in our pollen diagrams by the Primary Deforestation. This was their exploratory phase. After the Second Deforestation, however, the clearances follow each other with hardly any interval. It would therefore appear that their activities became more localised and the various clans or social units moved about within a relatively small area. Otherwise it would be necessary to suppose that subsequent to their exploratory period their population increased to such an extent that no area was free of occupation for long.

The beginning of the Second Deforestation at 275 cm. is less catastrophic than the first. From 275 cm., the *Plantago* curve climbs steadily towards higher values while *Ulmus* recedes slowly to reach a low value

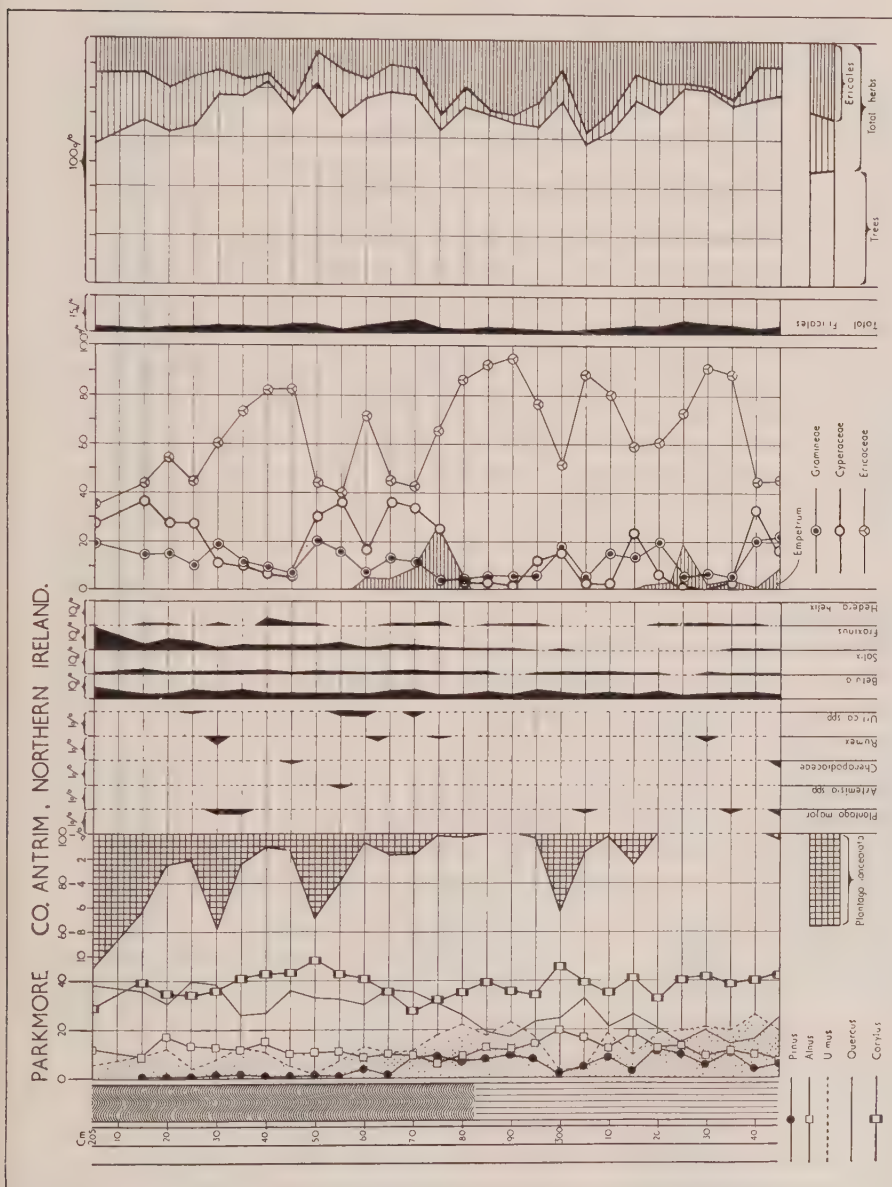


Fig. 4. A portion of Fig. 3 re-drawn in greater detail to illustrate the beginning of Neolithic deforestation. Percentages calculated as in Fig. 3.

at 250 cm., which is exactly opposite a well-marked maximum for *Plantago*. (This correlation between the *Ulmus* and the *Plantago* is so perfect that there can be no doubt that the two are related to the same event, as Iversen (1941) originally claimed.) Later, as the *Plantago* values decline, the *Ulmus* swings a little to the right indicating recovery. However, this is slight in comparison with recovery after the first clearance. There recovery could be described as complete. This apparent change in the regenerative ability of *Ulmus* is difficult to account for truthfully. It may be due to what seems the obvious cause here, namely the absence of a sufficiently long period of recovery. The Third Deforestation overlaps on the second. However, many workers would probably be inclined to invoke a climatic change to account for the behaviour of the *Ulmus* curve from this point onward in the diagram. In England this is a reasonable viewpoint since a climatic trend towards cooler conditions is indicated — at least so it would appear — by declining values of *Hedera* at the beginning of the Sub-Boreal period (Godwin, 1956). However, in Ireland the values of *Hedera* increase during the same period and, on the same argument, this would indicate a rise in temperature! However, in Ireland humidity rather than temperature may at this stage have controlled the expansion of *Hedera*. Further, the exact nature of the climate during the Sub-Boreal period in the British Isles (Godwin, 1956) — and elsewhere (Firbas, 1954) — is uncertain, and will become clear only as future studies uncover new facts. As far as Ireland is concerned, therefore, it is impossible to state categorically whether the long-term decline in *Ulmus* during Zone VIII, Mitchell's Pagan Period, was fundamentally climatic or anthropogenic in character.

From low values after the Second Deforestation *Plantago* recommences its climb to a fresh maximum which ushers in the Third Deforestation. And so the sequence ripples through the remainder of the pollen diagram, the clearances following each other in head-to-tail fashion. The main tree-pollen diagram illustrates clearly the long-term decline of *Ulmus* and shows that its place in the deciduous woodland appears to have been taken over by *Quercus*. From considering the relative behaviour of all the pollen curves it is obvious that this is not simply a replacement of the *Ulmus* by *Quercus* but represents a definite expansion of the latter. Again it is an open question whether or not this gradual expansion of the one genus and contraction of the other were fundamentally climatically or anthropogenically controlled.

Leaving further discussion of the "landnam" until later the next main feature of the main pollen diagram is the maximum of the oak curve at

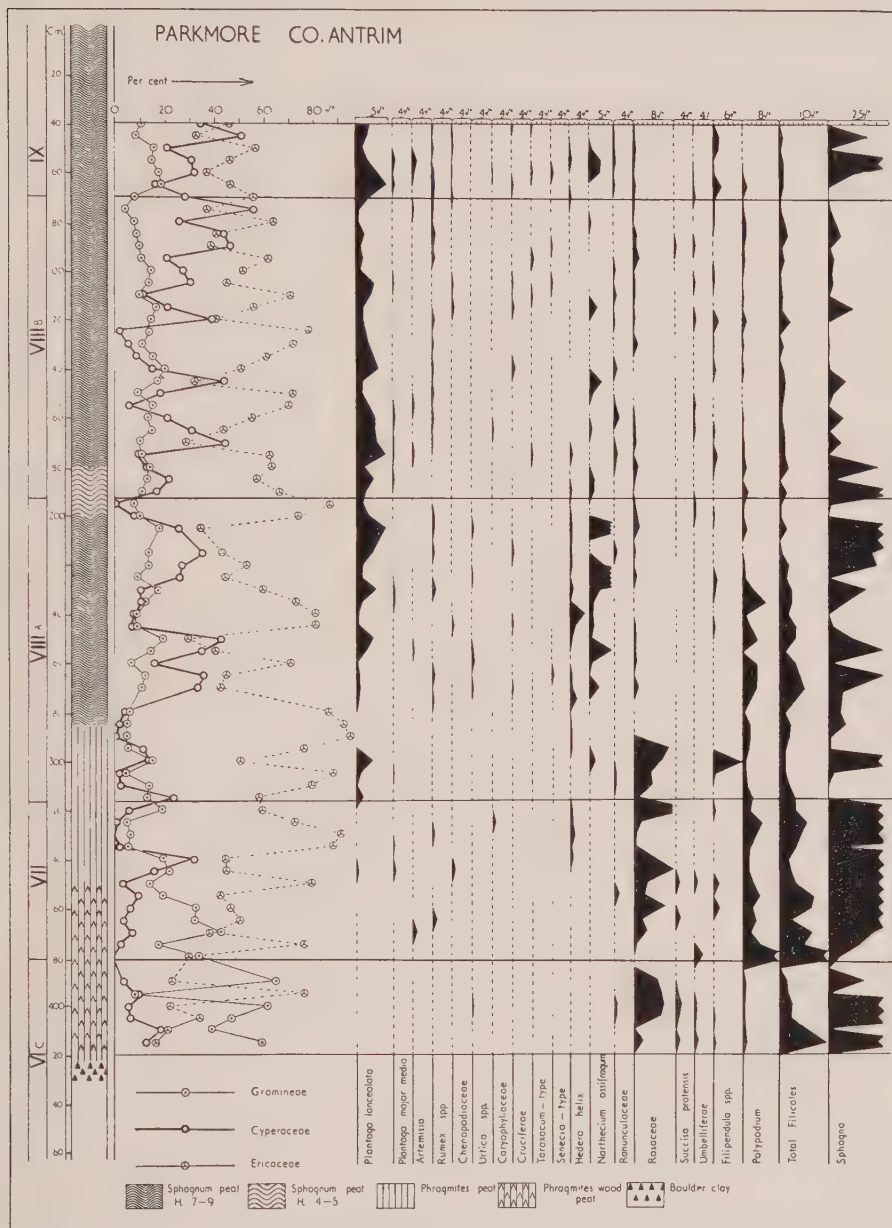


Fig. 5. Parkmore: non-tree pollen diagram. Percentages based on a total of the non-tree pollen but excluding aquatics and Pteridophytes.

200 cm. This is taken by Mitchell (1956) as marking the end of his Sub-zone VIII a, although he carefully points out that in those cases where the curve has a "spiky" character due to human interference it is possible that the absolute maximum may be displaced, and hence the VIII a/VIII b boundary may not always be synchronous. Carbon-14 assays of material just above and below the *Quercus* maximum led Mitchell (1958) to place the date of the transition around 1500 B.C.

It is interesting that in the present diagram the VIII a/VIII b transition occurs just above peaks of *Betula*, *Alnus*, and *Fraxinus*, and where the final disappearance of *Pinus* takes place. This level seems to have been a definite turning-point for the vegetation. One should notice too that new trends in the local bog vegetation begin at this level. Fig. 5 records a pronounced maximum of *Ericaceae* at 200 cm., and although the curve subsequently oscillates violently its further modes or peaks are succeeding lower and lower in value. Almost reciprocally the *Cyperaceae* are at a minimum at 200 cm., and then climb to higher values with successively greater and greater values. Thus a predominantly Ericaceous vegetation at the end of Sub-zone VIII a is gradually replaced by one in which *Cyperaceae* — perhaps *Scirpus caespitosus* — become more abundant. As the beginning of the *Cyperaceae* increase predates, by a long time, the introduction of extensive flocks of sheep, it probably reflects the more moist conditions during Sub-zone VIII b, which is more or less the former Sub-Atlantic period.

During Sub-zone VIII b there are no very strongly marked trends. On the whole *Quercus* and *Ulmus* tend to decline, while *Betula*, *Alnus*, *Corylus*, and *Fraxinus* increase. *Fraxinus* is interesting in the Irish diagrams since its first appearance in the Post-glacial period is after the Primary or Second Deforestation. This can be interpreted as meaning that the woodlands were previously of too closed a character for it to have grown in appreciable quantities. It is a tree having very high light-requirements. However, since in Denmark it first appears with the Mixed Oak forest during the Atlantic period it is surprising to have so little evidence of it at this time in Ireland. It serves to remind us of the extreme difficulty of generalising successfully in the biological world.

The increase of *Betula* in the Sub-Atlantic period is regarded by Danish palynologists as a response to forest clearance by fire. Birch would, it is believed, have been especially favoured by a "Slash and Burn" type of clearing since ashy soil is particularly suitable for the germination of the birch fruits. Godwin (1956), considering the British case, definitely

tends to lay less emphasis on fire and considers that a climatic cause had a larger role in its increase during the Sub-Atlantic period. He points to the consistency with which the increase takes place although deforestation progressed at different rates in different areas. He recalls that in the Somerset region birch increases noticeably at the Zone VII/VIII transition although later it shows little response to a definite intensification of agriculture in the vicinity.

Mitchell (1956) terminates Sub-zone VIII b with the final fall of *Ulmus*. But in many diagrams, including the present, *Ulmus* has fallen to low values at a much earlier date and it is therefore difficult to judge with accuracy the point of its final diminution. Perhaps, here it occurs at 70 cm., where *Alnus* is clearly at a minimum.

In the succeeding Zone IX, Mitchell's Christian Period, *Alnus* has a marked rise — also observable in many of the diagrams published by Jessen (1949) and Mitchell (1951, 1956). Towards the end of Zone IX *Alnus* customarily falls again and this final fall often coincides with the first indications of planted trees such as *Pinus* and *Fagus*. Apparently *Pinus* became extinct in Ireland sometime during the Sub-Boreal period, as in England and Wales, though in Scotland the pine forests of the present day seem to be truly native in status. In these woods a short-leaved, endemic *Pinus sylvestris* var. *scotica* maintains itself (Pearsall, 1950). The appearance of pollen of planted trees defines the opening of Mitchell's Zone X, the Afforestation Period. In the present diagram the IX/X transition cannot be found and lies presumably within the upper 40 cm., of peat which were not sampled on account of their unsuitable, loose texture.

Discussion

Iversen's (1941, 1949) interpretation of "landnam" assumed without question that the Neolithic deforestations occurred within a mixed deciduous woodland. That is a woodland in which — in this case — *Ulmus*, *Quercus*, *Tilia*, *Fraxinus*, *Corylus* and *Alnus* were freely intermingled to give a relatively undifferentiated or homogeneous formation. This is usually referred to as a Mixed Oakwood or Forest. The composition of the formation varies of course due to climatic, topographic, and historical factors. Thus in Ireland *Tilia* is absent, this genus occurring there today only as a result of recent introduction.

There is no difficulty in accepting the view that the Danish Stone Age settlements occurred within, literally, a mixed deciduous woodland. The

facts are hardly amenable to any other conclusion. We find that at the commencement of the deforestation the pollen curves for all the woodland genera, namely *Ulmus*, *Quercus*, *Tilia*, and *Fraxinus*, sink simultaneously and more or less to an equal or comparable extent. The settlement must have been established in a woodland where the genera were approximately randomly distributed. If they had been segregated into two or more associations then the clearing would, most likely, have affected some of the trees to a greater extent than others. Thus we can appreciate that the behaviour of the various pollen curves at the "landnam" event provides a means of *predicting* the former character or structure of the woodland. Normally, in a pollen diagram with no evidence of "landnam", this prediction or inference is impossible. The diagram records only the presence of various trees and shrubs but provides no indication of their original organisation into associations or association-segregates (Braun, 1935) on the former landscape.

Keeping these thoughts in mind let us now examine the present diagram (figs. 3 and 4) which is representative of the later Post-glacial period in the north-east of Ireland. A surprising discovery emerges. Here, unlike the examples from Denmark, the genera do not all behave alike at the onset of the deforestation phase. With each upsurge of *Plantago* the only tree which recedes consistently is *Ulmus*. *Quercus* which would have been expected to follow a parallel course very surprisingly rises to greater values! This relative behaviour of *Ulmus* and *Quercus* is almost invariably found in Irish pollen diagrams where agriculture is indicated by *Plantago* or other weeds such as *Rumex* and *Urtica*. This is a most interesting problem. There are two fairly obvious interpretations that may be examined. Stated in outline they are (a) that the *Ulmus* and *Quercus* were not randomly intermingled in the former woodland but grew more or less separately perhaps giving rise to two associations within the deciduous formation, and (b) that the woodland was truly of a mixed composition but the difference in the pollen record of *Ulmus* and *Quercus* arises from selective clearance, the Stone Age farmers having some special reason for sparing or conserving the oak. The second of these explanations has been touched on by Iversen (1949) and developed more fully by Troels-Smith (1953, 1954). Their viewpoints will be considered presently but first of all let us expand the ideas behind the first interpretation.

Ulmus and *Quercus* would have grown as separate associations if their soil requirements were sufficiently contrasting and if these contrasts found scope for expression among the soils developed in the Park-

more vicinity. This is an interesting possibility but difficult to examine thoroughly since it is uncertain which species of *Ulmus* and *Quercus* were native in Ireland during the period under discussion. Today *U. glabra* appears to be the native elm though perhaps *U. procera* and some other species which appear to have an endemic status in the British Isles (Godwin, 1956) cannot be entirely ruled out. However, as far as the soil requirements of elm are concerned it is not so necessary to know the actual species since all the elms are fairly basiphilous and require base-rich mull soils for successful regeneration. Such a generalisation would not suffice for the species of oak. Two species are regarded as native in the British Isles — *Quercus petraea* and *Q. robur*. *Q. petraea*, the Durmast oak, is a plant of shallow and acid soils and — according to Pearsall (1950) — constitutes about 98 per cent of the tree-flora in the natural upland British oakwoods. In Ireland too the remaining fragments of oakwood consist mostly of this species. On the other hand, *Q. robur*, the Lowland oak, is definitely more calcicole in character and occurs on deep clays and rich loams. These contrasting soil preferences of the two species are borne out by the accounts of the British oakwoods by Moss (1913), Salisbury (1916, 1918, 1921), and Salisbury and Tansley (1921). It is therefore not unreasonable to believe that *Quercus petraea* and *Ulmus glabra* would tend to have grown apart if contrasting soils were available. Over uniformly fertile soils, and such were perhaps predominant at Parkmore, elm would have developed as the dominant species. If, of course, *Q. robur* had been present either as well as *Q. petraea* or in its place, then it would undoubtedly have competed with the elm for the better soils and the outcome might have been a mixed community or mosaic. Obviously the question now is to determine which species of oak was in fact widespread in Ireland during the late Atlantic and early Sub-Boreal periods. This is difficult since the pollen of the two species cannot be separated, or so it is thought. Apart from this there are very few reliable identifications of sub-fossil macroscopic material. However such as there are indicate *Q. petraea*. Jessen (1949) has identified buds of this species from three Irish sites assigned to the Atlantic period. On the other hand there are no valid records of *Q. robur* from the Post-glacial period in either England or Ireland. Godwin (1956) notes though that there are numerous mentions of *Q. robur* but the identifications are valueless specifically since they were made at a time when there was no attempt to recognise *Q. petraea* as a valid species. He therefore places such records under the general heading "*Quercus*, Oak".

Obviously the evidence at present, although encouraging, is far too slight to allow a categorical statement. It is though very feasible so suggest as a working hypothesis that the ancient Irish deciduous woodlands comprised mainly *Ulmus* on the better soils, and *Quercus petraea* on the less fertile situations. Of course if there had been association-segregates of this kind they would not have escaped the notice of the Stone Age farmers. As well experience would have demonstrated to them that the richest soils for their cereal crops occurred where the elm grew luxuriantly. Naturally, therefore, they would have made their clearings in these stands and this would neatly account for the fact that *Ulmus* is the only tree which recedes consistently at the deforestation phases. *Quercus* would have remained unaffected and its contribution to the general spectrum of tree pollen would have increased along with that of other trees which were not cleared. Because its increase is very marked at each "landnam" one is inclined to believe that there was a real expansion of oak. Perhaps the Neolithic clearances impoverished the soils in their upper few inches so that once the area had been cleared of elm the seedlings of *Q. petraea* had a greater chance of success. Elm apparently regenerates only on the best mull soils. Godwin (1956) mentions that general soil deterioration might have been due to increased precipitation. This is a strong possibility since much of the blanket bog on the upland areas began to accumulate at this time. However, to set against this observation he notes that *Fraxinus*, which requires no less base-rich soils than *Ulmus*, expands at the same time as the last-mentioned recedes. But it must be remembered that *Fraxinus excelsior*, the native British ash, is in the first place a light-requiring species. It can grow on less fertile soils provided it is not overshadowed by other trees. Its pollen curve in the diagram is always slight but it is thought to be considerably under-represented.

The onus of proof for much of the present argument rests on demonstrating that *Q. petraea* was formerly the dominant Irish oak. Since macroscopic material is encountered so rarely there is an incentive for attempting to separate the pollen of *petraea* from that of *robur*. Erdtman (1948) has set down some observations on this point and it is obvious that the two pollens are very similar and whatever variation exists between them may be continuous. This is suggested also by the fact that fertile hybrids are known. Tansley (1939) has reported free hybridisation and intermediate forms in some areas of south-east England. However, according to Valentine (1951) hybridisation is fairly difficult when attempted artificially. He reports that in experiments recently

made by Dengler and others only about one per cent of the pollinations gave viable seed. He suggests that where the two species are sympatric in Europe ecological isolation — perhaps of the kind we have been discussing — is effective in curtailing hybridisation, and that this ecological isolation may be augmented by low interspecific compatibility. To determine whether or not the pollen of *Q. petraea* differs significantly from *Q. robur* it might be worth having an electron microscope study. This should indicate if their separation would really be practical under the optical microscope. Bradley (1958) has made something of this approach to the well-known case of the pollen of *Myrica* and *Corylus*.

The alternative approach to the contrasting behaviour of *Ulmus* and *Quercus* in the Irish diagrams is through the theory of selective felling or selective utilisation. This theory would suggest that *Ulmus* was selectively removed while *Quercus*, for some reason, was permitted to remain. Speculations along these lines have been made to some extent by Iversen (1949) but more particularly by Troels-Smith (1953, 1954). Iversen (1949) resorted to this theory for an answer to some of Nilsson's (1948) queries about his original (1941) interpretation of "landnam" in the Danish diagrams. Nilsson was not convinced that the diminution of the deciduous woodland had been due to prehistoric deforestation and he was more inclined to favour an explanation in climatic terms. He noted that *Ulmus* and *Tilia* — both fairly thermophilous trees — were affected more seriously than *Quercus*. (It should be mentioned, to avoid confusion and misunderstanding, that the difference in behaviour of elm and oak during the Danish "landnam" phases is relatively slight and by no means so striking as in Ireland.) Iversen suggested that perhaps *Quercus* had been spared on account of its valuable hog-fattening mast, or may have been untouched simply because its wood was so much more difficult to cut than that of elm or lime. The second of these suggestions is very plausible but it is questionable if the first is realistic. Even if we concede that swine formed an important part of the Neolithic economy it seems unlikely that in a virgin forest there would have been any need to conserve the oak trees within the area of settlement. By themselves these would hardly have sufficed for the nourishment of the swine and surely these are more likely to have sought their food as they roamed in the adjacent glades.

Troels-Smith's viewpoint on this problem is more formidable, though this is largely due to the fact that he brings a considerable body of ethnobotanical data in support of his ideas. He is strongly of the belief that the Neolithic settlements were within truly mixed deciduous wood-

land composed of oak, elm, ash, lime, and hazel. He believes, however, that the Stone Age farmers employed these trees in various ways. He particularly asserts that elm was an important fodder item for the cattle. These were fed on leaves and young branches. The pruning of the trees for these items would have sufficed to reduce the number of flowering branches and this would have resulted in the diminution of elm pollen which is recorded in the diagrams. Nordhagen (1954) has noted that elm branches require to be at least nine years old before they can produce flowers. Thus, persistent harvesting of newly produced shoots would certainly have eliminated pollen production. On the other hand the leaves of oak are valueless for fodder and hence its branches would have been untouched. The increase of oak pollen in the diagrams is thus to begin with a proportional or apparent increase. However, the increase is so marked that more than this must be the cause. Troels-Smith is inclined to believe that the removal of a few trees and shrubs in the clearing allowed more light to reach the remaining oaks and this greatly stimulated their flowering. Where *Tilia*, or lime is also recorded it generally recedes along with the *Ulmus* and Troels-Smith has suggested that its leaves may also have been used as fodder while its bast perhaps was manufactured into ropes and strings. So far, Troels-Smith (1953, 1954) has only outlined his views on this interesting topic and he has yet to publish, I believe, extensive evidence. Even in a preliminary form we must admit that his arguments are entirely plausible and are — as we have noted — supported by ethnobotanical data (Nordhagen, 1954; Ve, 1930).

The record of "landnam" in the Irish diagrams has now been submitted to two theories. In the first I have suggested that contrasting soil needs of the original species of elm and oak led to the development of relatively distinct associations within the deciduous woodland formation. In the second we have outlined what may almost be called Troels-Smith's Theory of Selective Utilisation. At present no means exist for determining which thesis holds the greatest measure of truth. One of the valuable features of the first thesis is that it draws attention to the fact that there are no compelling *a priori* reasons for maintaining that the deciduous woodland in the Irish Post-glacial was a homogeneous or undifferentiated mixture of genera. It is salutary to remember that edaphic variations combined with physiographic and climatic gradients — which we believe to have existed — would tend in most circumstances to prevent the development of the ideal undifferentiated climax vegetation. The palaeo-ecologist may perhaps fall into fewer pitfalls if his

interpretations are guided by a philosophy which accepts climaxes in nature as, generally, aggregates of associations and, as Braun (1935) terms them, association-segregates.

Summary

1. The stratigraphy and pollen analysis of a Post-glacial profile from Parkmore, in the north-east of Ireland, are described.
2. The pollen diagram is discussed and zoned according to the system of pollen zonation recently proposed for Ireland by Mitchell (1956).
3. Deforestation phases by Neolithic and later cultures are very clearly recorded in the diagram.
4. These deforestation phases are described and an attempt at their interpretation involves the discussion of two hypotheses.

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Zur Systematik der Desmidiaceen

Von ROLF GRÖNBLAD und JIŘÍ RŮŽIČKA

Karis, Finland und Třeboň, Tschechoslowakei

»The first rule which cannot be emphasized often enough is that we should name populations, not individuals . . .»

Ernst Mayr (1942, p. 16).

I. Einleitung

Bekanntlich herrscht in der Algologie betreffs der taxonomischen Termini und der Grundsätze zu ihrer Benützung im gegenwärtigen Stadium grosse Willkür. So werden auch die Desmidiaceen, die doch eine verhältnismässig gut bekannte und bearbeitete Gruppe bilden, vom taxonomischen Standpunkte aus von verschiedenen Autoren höchst unterschiedlich beurteilt, worin einer der Gründe der Unklarheit und Verwirrung in ihrer Systematik liegt.

Die Verfasser dieses Aufsatzes haben die Möglichkeiten erwogen, wie sich dieser Zustand in eine bessere Ordnung bringen liesse. Einige ihrer Erwägungen legen sie in diesem Aufsatz vor, wobei betont sei, dass sie keineswegs glauben, eine endgültige Lösung gefunden zu haben. Einige diesbezügliche Probleme scheinen jedoch in der Algologie schon höchst dringlich zu sein, und so hoffen die Autoren, wenn auch alle Einzelheiten dieses Aufsatzes keine Zustimmung finden werden, dass er wenigstens einen Ausgangspunkt für weitere Diskussionen bilden möge. Als Desmidiologen berühren sie hier nur die Systematik der Desmidiaceen. Der Leser möge selbst erwägen, inwieweit damit auch die Systematik anderer Algengruppen betroffen wird.

In der Systematik der Desmidiaceen sollten unserer Meinung nach folgende Grundsätze beachtet werden:

1. Die Definitionen der einzelnen Taxa sind heutzutage schwer zu formulieren, und ihre Begrenzung muss deshalb der subjektiven Auffassung der einzelnen Forscher überlassen werden. Es ist jedoch zu

empfehlen, dass die ganze Variabilitätsbreite eines jeden Taxons gewissenhaft erforscht wird, und dass bei einem sich ergebenden Zweifel der Umfang eines Taxons eher breiter als zu eng aufgefasst wird.

2. Wir halten es für selbstverständlich, dass nur ständige, d.h. auch auf die Nachkommenschaft übertragbare Abänderungen als Taxa (als selbständige systematische Einheiten) aufgefasst und bezeichnet werden sollen.

3. Zur Bezeichnung einer ständigen Abänderung sollen von den in dem Internationalen Code der botanischen Nomenklatur aufgezählten taxonomischen Termini nur eine kleine Anzahl benutzt werden, nämlich Art (*species*), Varietät (*varietas*) und Form (*forma*), und dazu noch, falls unbedingt notwendig, Unterart (*subspecies*).

4. Falls es einem Autor als unentbehrlich erscheint, auch die vorübergehenden und nichtbeständigen Abänderungen oder Zustände zu registrieren und zu bezeichnen, so dürfen für diesen Zweck keine taxonomischen Termini (z.B. „*forma*“) benutzt werden; es können dafür aber andere, nichttaxonomische Termini gebraucht werden (z.B.: „*modificatio*“, „*morpha*“, „*facies*“, „*monstrositas*“ usw.).

5. Wir nehmen uneingeschränkt Stellung gegen die Unsitte, jede unbedeutende Abänderung, besonders aber solche nichtständiger Natur, mit einem Epitheton zu benennen und mit dem Namen ihres Autors zu versehen.

In diesem Aufsatz werden einige dieser Grundsätze näher besprochen und an Beispielen aus der Reihe der Desmidiaceen erläutert. Er entstand als Resultat eines längeren Schriftwechsels zwischen den beiden Autoren. Prof. Dr. P. Kallio, Turun Yliopisto, und Dr. J. Komárek, Praha, haben freundlicherweise das Manuskript sorgfältig durchgelesen und viele wertvolle Bemerkungen beigefügt; hierfür sei ihnen herzlichst gedankt.

Bezüglich unserer Terminologie sei noch angeführt, dass wir in dem Aufsatz den in der biotaxonomischen Literatur geläufigen Ausdruck „Abänderung“ gebrauchen. Als „Abänderung“ (auch „Abweichung“) bezeichnen wir ein bestimmtes konkretes Individuum, welches sich von den anderen unterscheidet, oder auch eine Gruppe von Individuen, welche in einem gemeinsamen Merkmale von den anderen abweicht, dessenungeachtet, ob es sich um ständige oder nichtständige, zufällige oder gesetzliche, durch äussere oder innere Einflüsse verursachte Merkmale handelt. In diesem Aufsatz werden wir uns mit den Abänderungen vom Gesichtspunkte der Taxonomie und Nomenklatur aus befassen.

II. Über den Grad der Variabilität der Taxa

Wenn wir den ersten oben festgesetzten Grundsatz überlegen, müssen wir eingestehen, dass wir heute noch nicht in der Lage sind, einige grundlegende taxonomische Begriffe einheitlich aufzufassen, geschweige die einzelnen Taxa selbst. Der Internationale Code vermeidet ausdrücklich, sie zu definieren (Präambel, p. 11).

Von den bisher geltenden Regeln (Art. 25; Int. Code 1956, p. 25) kann man aber wenigstens den wichtigen Grundsatz ableiten, dass sämtliche taxonomischen Einheiten gleicher Kategorie, welche zu einem bestimmten höheren Taxon gehören (z.B. sämtliche Varietäten derselben Art), taxonomisch gleichwertig sind. Dadurch verschwindet der Unterschied zwischen der bevorzugten „typischen“ Form (in der älteren Literatur manchmal als „*forma typica*“, „var. *genuina*“ bezeichnet) und den sonstigen Abänderungen, welche früher dieser „typischen“ Form nur als blossе Ausnahmen von der Regel zugeordnet wurden. Sobald irgendeine Art (oder ein anderer Taxon) in niedrigere Kategorien geteilt wird, kann kein Individuum derselben Art ausserhalb dieser niedrigeren Kategorien stehen. Falls z.B. ein Autor die Art *Tetmemorus granulatus* Bréb. (ex Ralfs) nur in drei Varietäten teilen will, var. *granulatus*, var. *attenuatus* W. West und var. *elongatus* Krieg., so muss er sich dessen bewusst sein, dass diese drei Varietäten vom taxonomischen Standpunkte aus gleichwertig sind und dass jedes zu dieser Art gehörige Individuum unter irgendeine von diesen Varietäten eingliedert werden muss.

Moderne Arbeiten zeigen immer deutlicher, dass das, was wir in der Algologie als Art zu benennen pflegen, in Wirklichkeit ein Komplex von morphologischen, anatomischen, physiologischen, ökologischen und geographischen Abänderungen ist. Den jeweiligen Abänderungen werden von den einzelnen Autoren verschiedene Namen beigelegt, und sie werden sehr verschiedenartig aufgefasst und definiert.

Der Umfang des Grades der Variabilität ist bei den Algen noch sehr wenig bekannt. Es gibt jedoch Anzeichen dafür, dass die Variabilitätsbreite bei einer Art recht bedeutend sein kann, namentlich in den morphologisch stark verschiedenförmigen Gruppen (wie bei den Desmidiaceen), wo sie leichter feststellbar ist.

Als Beispiel kann die abgebildete Serie von Zeichnungen dienen (Fig. 1—8), die einige von einem einzigen Fundorte herrührende Exemplare von einer Art der Gattung *Staurostrum* darstellen. Es ist ersichtlich, dass etliche morphologische Merkmale hier auffallend übereinstimmen (be-

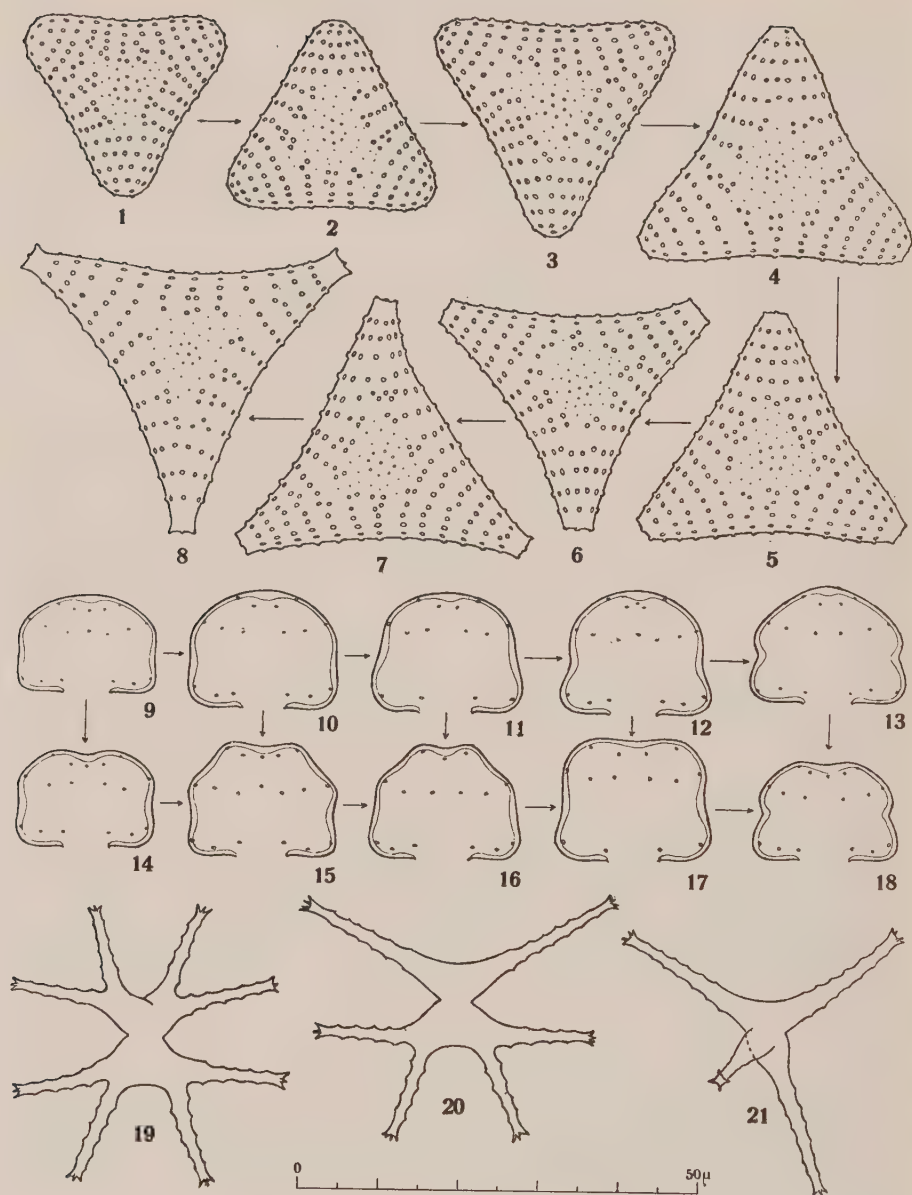


Fig. 1—8. *Staurostrum dispar* Bréb. (?). 9—18. *Cosmarium difficile* Lütkem. (nach Růžička). 19—21. *Staurostrum bibrachiatum* Reinsch (nach Scott und Grönblad).

sonders die Skulptur und die Dimensionen des inneren Zellteiles), wogegen bei anderen eine kontinuierliche Serie von Übergangsformen besteht. Folglich ist die Überzeugung berechtigt, sämtliche, hier abgebildete Exemplare einem einzigen, sehr breit variablen Taxon, jedenfalls einer einzigen Art zuzuordnen. Die voneinander abweichenden Formen, namentlich die beiden äussersten (Fig. 1 und Fig. 8), sind jedoch habituell sehr verschieden; es ist kein Wunder, dass Autoren, welche dieselben isoliert gefunden oder beurteilt haben, sie als mehrere selbständige Arten bestimmt haben.¹

Ein weiteres Beispiel bildet eine Serie von Zeichnungen der variablen Halbzellenform bei der Art *Cosmarium difficile* Lütkeim. (Fig. 9—18); die Exemplare gehörten auch zu einer Population. In der Literatur sind noch weitere Fälle angeführt. Siehe z.B. die interessante Variabilität der Art *Staurastrum minnesotense* Wolle, wiedergegeben in den Figuren von Grönblad (1945, Fig. 231—235) und Scott und Grönblad (1957, Tab. 34, Fig. 4—10), der *Arthrodesmus subulatus* Kütz. in Scott und Grönblad (1957, Tab. 11, Fig. 7—21) und der *Cosmarium subquadratum* Nordst. in Wehrle (1953, Fig. 1—35). Die ganze oder beinahe vollständige Variabilitätsbreite wird leider nur sehr selten so eingehend aufgenommen.

Aber nicht nur die äussere Zellenform, auch die innere Organisation ist manchmal recht variabel. Aus den beigegeführten Abbildungen sind Fälle der Variabilität des Chromatophorenbaues bei *Cylindrocystis brebissonii* Menegh. ex de Bary var. *minor* W. et G. S. West (Fig. 22—31) und *Spirotaenia obscura* Ralfs (Fig. 32—34) ersichtlich. Wir weisen auch auf die recht veränderliche Anzahl der Pyrenoide und der Gipskristalle bei den *Closterium*-Arten hin, die bisher in den Monographien öfters genau angegeben werden, obwohl es sich hierbei um ein sehr variables und manchmal taxonomisch wertloses Merkmal handelt.

Es gibt nur wenige Fälle, bei denen man auf Grund natürlichen Materials eine weitgehende Variabilität im Rahmen eines einzigen Taxons zeigen kann. Meistens stehen uns nur vereinzelte Bruchstücke derartiger kontinuierlicher Reihen zur Verfügung. Immerhin ist uns in dieser Frage doch soviel bekannt, um begründet vorzuschlagen, dass die Bearbeiter stets die ganze Variabilitätsbreite der Taxa erforschen sollen, auch dort, wo nur eine einzige, sehr begrenzte Form vorzuliegen scheint.

Ehe die Frage der Variabilitätsbreite vollkommen gelöst sein wird,

¹ Die genaue systematische Beurteilung erfordert hier noch ein weiteres Studium der älteren Literatur; vielleicht kann sie als *Staurastrum dispar* Bréb. 1856 bezeichnet werden.

ist es vorläufig selbstverständlich notwendig, auch kleinere Abänderungen zu registrieren, d.h. kurz zu beschreiben und namentlich genau abzubilden. Wichtig sind besonders solche Abänderungen, welche (tatsächlich oder nur scheinbar) einen Übergang zwischen zwei taxonomischen Einheiten bilden (z.B. Fig. 2—7, Fig. 10 u.dgl.); ihr Studium ermöglicht uns nämlich oft, die wirkliche Variabilitätsbreite zu beurteilen und die richtige Grenze der einzelnen taxonomischen Einheiten zu bestimmen.

Dagegen ist es jedoch keineswegs notwendig, sogar unzulässig, dass solche Abänderungen auch benannt werden sollten. Wir möchten hier auf das Beispiel des hervorragenden schwedischen Algenforschers Dr. O. Borge hinweisen; er suchte nicht jede Abänderung zu benennen, die er nicht mit gutem Gewissen für eine selbständige Einheit halten konnte, sondern bezeichnete solche Abänderungen nur als „forma“, ohne ein Epitheton hinzuzufügen. Er hat sie jedoch immer beschrieben und grösstenteils auch abgebildet. Deshalb behalten seine Arbeiten ihren Wert und ihre Brauchbarkeit sowohl für die Gegenwart als auch für die Zukunft.

III. Taxonomische und nichttaxonomische Abänderungen

Der Internationale Code der botanischen Nomenklatur lässt bisher eine überaus breite Auffassung des Begriffes „Taxon“ zu. Im Vorwort (Präambel, I. Abschnitt, Code 1956, p. 11) verzichten die Verfasser auf das Recht, den Inhalt einzelner taxonomischer Kategorien festzustellen und im Art. 24 (l.c., p. 24) sprechen sie unter der Bezeichnung „infraspecific taxa“ sogar auch über unbedeutende und vorübergehende Abänderungen („slight or transient modifications of wild plants“). Als eine selbständige taxonomische Einheit kann sonach (bis auf geringfügige Ausnahmen, z.B. Monstrositäten, siehe Art. 67 des Codes) jede, wenn auch unbedeutende und durchaus unbeständige Abänderung beschrieben werden. Diese Freiheit führt in der Praxis zu einem lawinenartigen Anwachsen von neuen und immer neueren Taxa und Namen. Hier zeichnet sich bereits ein schwerwiegendes Problem der heutigen Desmidiologie ab, dessen Lösung man nicht mehr aufschieben darf.

Um diesem ständigen Anwachsen der Unübersichtlichkeit und der Unklarheit des Systems vorzubeugen, halten wir es für notwendig, zwei vom taxonomischen Gesichtspunkte aus prinzipiell verschiedene Abänderungen, nämlich die taxonomischen von den nichttaxonomischen konsequent zu unterscheiden.

Unserer Ansicht nach können nur ständige, auch auf die Nachkommenschaft übertragbare, erblich fixierte Abänderungen als taxonomisch betrachtet werden.

Bisher pflegten die Autoren beide Abänderungen willkürlich zu bezeichnen. Wir haben uns der Ansicht angeschlossen, dass es zu einer steigenden Verwirrung der Nomenklatur und Systematik und zu einem unerträglichen Anwachsen des Namens- und Synonymenverzeichnisses führt, wenn man für beide Sorten von Abänderungen dieselben Termini (z.B. „forma“) benutzt. Wir empfehlen dringend, dass beide Sorten mit ganz verschiedenen Termini bezeichnet werden.

Es ist manchmal sehr schwer zu entscheiden, ob eine bestimmte, in der Natur gefundene Abänderung ständig und sonach taxonomisch ist, also nach einer gewissen Zeit nicht in eine andere übergeht. Die Methoden zur Feststellung der Ständigkeit der Abänderungen sind aber bisher ebenso mühselig wie unvollkommen, und die Mehrzahl der Forscher wird sich deshalb nur nach eigenen Erfahrungen ein Urteil bilden — und das ist, leider, manchmal sehr subjektiv. Wir müssen uns noch für eine lange Zeit statt eines exakten Beweises nur mit einer begründeten Vermutung des jeweiligen Bearbeiters begnügen. Es gibt zwei verschiedene Methoden zu diesem Zweck: 1) die statistische Bearbeitung von umfangreichem natürlichem Material und 2) Reinkulturen.

Man könnte somit einwenden, es sei für eine terminologische Unterscheidung der beiden Sorten von Abänderungen noch genügend Zeit, bis man sie in Wirklichkeit wird unterscheiden können. Diesen Einwand halten wir für nicht gerechtfertigt. Vor allem kennen wir schon heute eine ganze Reihe von zweifellos nichtständigen Abänderungen. In den übrigen vorläufig noch unklaren Fällen wird es sich als vorteilhaft erweisen, wenn der Forscher vor die Notwendigkeit gestellt wird, sich für diese oder jene Sorte von Termini zu entscheiden; er wird sich dabei mit der Frage befassen müssen, inwieweit die festgestellte Abänderung wahrscheinlich ständig oder nichtständig ist, und schon dieser Umstand wird einer Publizierung von immer neueren Taxa eine Grenze bieten. Es ist wahr, dass unsere Kenntnisse in der Frage der Ständigkeit oder Nichtständigkeit bisher sehr unvollständig sind. Dies ist jedoch kein Beweggrund dafür, dass wir, wenn auch nur auf Grund unserer bisherigen Kenntnisse, einen logischen Aufbau des Systems nicht jetzt schon anstreben sollten.

IV. Taxonomische Abänderungen

Vor allem taucht die Frage auf, wieviel infraspezifische taxonomische Kategorien und somit auch Termini für die Einteilung einer bestimmten Algengruppe erforderlich sind. Einige Autoren sind der Ansicht, dass ausser der Art (*species*) nur eine einzige niederere Kategorie angewendet werden soll (z.B. Poľanskij, 1956). Bei manchen Algengruppen, z.B. Cyanophyceen, kann man sich tatsächlich mit einer einzigen solchen Kategorie begnügen. Bei den morphologisch mehr differenzierten Algen, wie bei den Desmidiaceen, kann man jedoch mit einer einzigen infraspezifischen Kategorie nicht auskommen; wir empfehlen hiermit die Benützung von zwei Kategorien, und zwar „*varietas*“ und „*forma*“. Dagegen betrachten wir den Fachausdruck „*subspecies*“, der von den älteren Desmidiologen mehrmals gebraucht wurde, in der heutigen Desmidiologie als nicht unbedingt nötig. Freilich lässt sich nicht verbürgen, dass in der Zukunft, wenn unsere Kenntnisse von der Entwicklung und den Lebensvorgängen der Desmidiaceen eingehender analysiert sind, sich nicht auch die Notwendigkeit einer dritten infraspezifischen Kategorie zeigen könnte.

Den taxonomischen Kategorien und Termini darf in keinem Falle ein nichttaxonomischer Inhalt beigelegt werden. Fälle, wo in der Literatur unbeständige Abänderungen, ja manchmal auch Monstrositäten und Zustände als „*subspecies*“, „*varietas*“, am häufigsten aber als „*forma*“ bezeichnet werden, sind konsequent zurückzuweisen.

Die Hierarchie der Taxa, d.h. die Rangordnung der *species* — (*subspecies*) — *varietas* — *forma*, muss freilich unbedingt eingehalten werden (Art. 5 des Intern. Code, 1956, p. 13); dagegen ist es zulässig, einige der niedereren Kategorien wegzulassen. Demnach ist es möglich, eine Art in die gleichwertigen Unterarten oder direkt in Varietäten, diese wieder in Formen oder eine Art direkt in Formen einzuteilen. Die gegenseitig ungleichwertigen Kategorien (z.B. sowohl Varietäten als auch Formen) dürfen nicht untereinander gemischt und gleichzeitig angewandt werden. Dass die Art (und die übrigen Taxa) laut der jetzt geltenden Regeln in niedrigere Kategorien restlos zerfallen, wurde bereits betont.

Die Existenz von taxonomischen Abänderungen (*subspecies*, Rassen) innerhalb eines begrenzten geographischen Areales ist bei den Desmidiaceen bisher noch nicht unstreitig erwiesen. Manche Autoren betrachten sie jedoch als wahrscheinlich, vgl. z.B. Krieger (1933, p. 106), Messinkommer (1942, p. 401), Grönblad (1945, p. 6). (Selbstverständlich sehen wir hier von jenen Abänderungen ab, welche an solche bestimmte Be-

dingungen gebunden sind, die nur in einem begrenzten Areal z.B. nur in den Tropen vorkommen.)

Ein interessanter Fall sei hier erwähnt. *Xanthidium superbum* Elfv. wurde zuerst aus Finnland von Elfving (1881) beschrieben und später von Grönblad (1938) neugefunden. Dieselbe Art ist sonst nur aus Australien (Borge, 1896) und jüngst aus Australien und Indonesien her (A. M. Scott und C. W. Prescott, 1958 und A. M. Scott in litt.) bekannt. Deren Variabilität ist aber trotz den ganz verschiedenen Fundorten und wohl auch Lebensbedingungen unerwartet gering.

Theoretisch genommen gibt es keinen Grund, warum jede stabile, wenn auch unbedeutende Abänderung nicht als Taxon bezeichnet und benannt werden könnte (Art. 24 des Code). Es ist aber fraglich, ob dies in der Praxis wünschenswert wäre. Der Ausbau eines derartigen Systems von stabilen, jedoch unbedeutenden Abänderungen würde eine unübersehbare Menge von Arbeitskräften und Zeit erfordern und das Ergebnis wäre ein monströses, sogar für den Fachmann nichtbeherrschbares und in der Praxis ganz unbrauchbares System.

Es ist somit geboten, das Recht der Autoren, eine neu festgestellte stabile Abänderung zu benennen, einzig und allein auf unbedingt nötige Fälle zu beschränken, d.h. auf Fälle, bei denen es sich um eine genügend bedeutungsvolle und schwerwiegende Abänderung handelt. Die Beurteilung der Wichtigkeit irgendeiner Abänderung ist derzeit selbstverständlich hauptsächlich von der Gewissenhaftigkeit einzelner Autoren abhängig. Der von einigen Bearbeitern gepflogene Brauch, eine jede wertlose Abänderung zu benennen und mit Autorennamen zu bezeichnen, sollte ein für allemal energisch abgelehnt werden.

Freilich sollte auch das andere Extrem vermieden werden: nämlich die Bildung von sogenannten „Sammelarten“, welche einige morphologisch ähnliche, in Wirklichkeit aber unverwandte Taxa einbeziehen. Solche Sammelarten führen in der Praxis zur Verwechslung von ökologisch verschiedenen Organismen. Bei den Desmidiaceen kann man als Sammelarten z.B. zahlreiche „Arten“ nach Klebs' und Playfairs Auffassung bezeichnen, von den neueren Arbeiten z.B. *Closterium intermedium* Ralfs sensu Krieger 1935, *Pleurotaenium trabecula* (Ehr.) ex Näg. und *Pleurotaenium ehrenbergii* (Bréb.) ex de Bary sensu W. et G. S. West 1904 und Krieger 1937, *Staurostrum gracile* Ralfs sensu W. et G. S. West et N. Carter 1923, weiter *Arthrodesmus incus* (Bréb.) Hass. ex Ralfs, dessen zahlreiche „Varietäten“ kaum untereinander verwandt sind, und manche andere.

V. Nichttaxonomische Abänderungen

Die zweite grosse Gruppe von Abänderungen bilden die nichttaxonomischen Abänderungen. Wie bereits erwähnt, sollen unserer Ansicht nach als solche die unbeständigen, d.h. auf die Nachkommenschaft nicht übertragbaren Abänderungen angesehen werden.

Einzelne nichtständige charakteristische Abänderungen kommen oft nicht nur bei einem gewissen Taxon (z.B. nur bei einer gewissen Varietät) vor, sondern erscheinen manchmal bei der ganzen Artengruppe oder auch Gattung. So kann z.B. eine gewisse durch abnormale Zellteilung oder Zellwachstum entstandene unbeständige und nichtvererbliche Abnormität (Fig. 37) nicht nur bei der ganzen Art *Tetmemorus laevis* (Kütz.) ex Ralfs einschliesslich aller ihrer Varietäten und Formen zum Vorschein kommen, sondern auch bei sämtlichen sonstigen Arten derselben Gattung, ja sogar bei der verwandten Gattung *Euastrum*. Die sigmoiden Zellenformen (Fig. 35) kommen bei der Mehrzahl der *Closterium*-Arten und auch bei einigen anderen Gattungen vor. Die polyradiaten Facies (Fig. 39) können bei den meisten Desmidiaceengattungen angetroffen werden usw. Es ist sonach klar, dass die nichtständigen Abänderungen gänzlich ausserhalb der Hierarchie der Taxa stehen; die Versuche, sie in diese Hierarchie einzugliedern, endeten mit einem Misserfolg („subspecies“ und später „facies“ sensu Teilung, s. weiter unten).

Die nichttaxonomischen Abänderungen sollen niemals mit taxonomischen Termini (z.B. „forma“) bezeichnet werden, wie dies schon früher betont wurde. In einigen Fällen kann es aber doch wichtig sein, auch eine nichttaxonomische Abänderung irgendwie zu bezeichnen; z.B. kann sie als Indikator äusserer Umstände von Bedeutung sein. Falls es somit überhaupt als notwendig erscheint, können die nichtständigen Abänderungen mit den nichttaxonomischen Termini bezeichnet werden.

In der Literatur wird für die nichtständigen Abänderungen seit Jahren der Terminus „modificatio“ gebraucht, der bereits festen Fuss gefasst hat. In dem ursprünglichen Sinne wird jedoch dieser Fachausdruck nur für die ausgesprochen ökologisch bedingten Abänderungen benutzt. Růžicka (wie manche andere tschech. Algologen) führt ein und benutzt noch als einen breiteren Terminus den Fachausdruck „morpha“ (Semenov Tan-Šanskij, 1910), der sämtliche nichtständige Abänderungen, von deren Ursache abgesehen, umfassen soll. Gewisse Anomalien können als „monstrositas“ oder „abnormitas“ bezeichnet werden. Für die nichtständigen Abänderungen in der Zahl der Symmetrieebenen hat Teiling

1952 den Terminus „facies“ eingeführt. Mit diesen genannten Termini sind natürlich alle Möglichkeiten nicht erschöpft.

Wir sind vollkommen überzeugt, dass die nichtständigen Abänderungen weder mit einem Epitheton benannt noch mit dem Namen des Autors bezeichnet werden sollen. Demgegenüber erscheint es als zulässig, sie zu beschreiben, eventuell auch mit einem lateinischen Satze oder sogar mit einem einzigen lateinischen Adjektivum. Eine solche Beschreibung soll jedoch weder als Diagnose, noch als Benennung im Sinne des Intern. Code für botanische Nomenklatur gehalten werden; die Endsilbe eines solchen eventuellen Adjektivums soll sich nicht nach dem grammatischen Geschlecht der Benennung der Alge richten, und es soll auch nicht kursiv gedruckt werden, wie dies bei den Namen der Organismen üblich ist.

So ist z.B. die schon erwähnte Abnormität der Art *Tetmemorus laevis* (Kütz.) ex Ralfs (Fig. 37) als „var. *bifidus* Gutw. 1890“ beschrieben worden: sie ist jedoch in Wirklichkeit kein Taxon und im Sinne der vorgeschlagenen Regeln sollte ihre Bezeichnung, falls überhaupt notwendig, lauten: „*Tetmemorus laevis* (Kütz.) ex Ralfs morpha apicibus bifidis“, oder kürzer „morpha bifida“, keineswegs aber „morpha *bifidus* (Gutw.) comb. nova“. Anstatt „morpha“ kann natürlich auch ein anderer nichttaxonomischer Terminus gewählt werden, z.B. „monstrositas“, („cellula monstrosa“).

Im folgenden werden jetzt einige bei den Desmidiaceen öfter vorkommende nichtständige Abänderungen näher besprochen.

Zu den unbeständigen und auf die Nachkommenschaft nicht übertragbaren Abänderungen gehören zunächst verschiedene teratologische Änderungen, Anomalien und Monstrositäten, die bei den Desmidiaceen sowohl in der Natur als auch in den Kulturen erscheinen. Gewöhnlich geschieht dies infolge von Unregelmässigkeiten in der Teilung oder beim Wachstum der Zellen. In diesen Erscheinungen spiegelt sich oft die Einwirkung des äusseren Milieus ab.

Solche Abnormitäten hat man früher oft als Taxa beschrieben und mit einem Namen versehen, wie es bei dem oben erwähnten *Tetmemorus*, oder bei *Micrasterias crenata* Bréb. und *M. rabenhorstii* Kirchn. der Fall ist, die in Wirklichkeit nur Abnormitäten von *M. truncata* (Corda) ex Bréb. resp. *M. crux-melitensis* (Ehr.) Hass. ex Ralfs darstellen.

Jetzt verwirft der Internationale Code 1956 (Art. 67 p. 43) ausdrücklich solche Namen und Taxa, die auf einer Monstrosität beruhen. Heute würde deshalb wohl kaum ein ernsthafter Autor zu finden sein, welcher die Berechtigung solcher Abnormitäten als Taxa vertreten wollte. In der

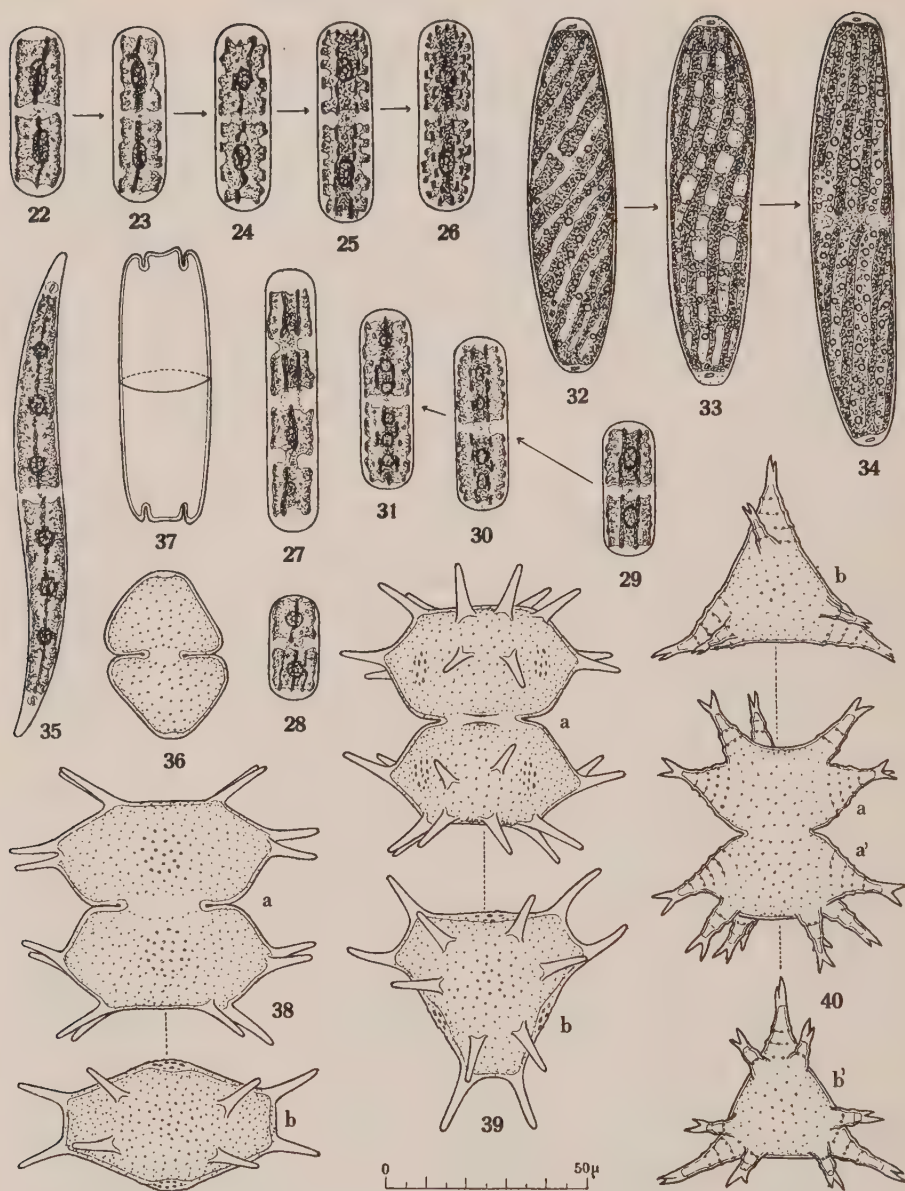


Fig. 22—31. *Cylindrocystis brebisonii* (Menegh.) De Bary var. *minor* W. & W. 32—34. *Spirotaenia obscura* Ralfs. 35. *Closterium* sp., sigmoide Abänderung. 36. *Cosmarium granatum* Bréb., asymmetrische Abänderung. 37. *Tetmemorus laevis* (Kütz.) Ralfs, Monstrosität (nach Gutwiński). 38. *Xanthidium antilopaeum* (Bréb.) Kütz. 39. *Xanthidium antilopaeum* fac. 3, („var. *triquetrum* Lund.“). 40 a—b. *Staurastrum furcigerum* Bréb. 40 a'—b'. *Staurastrum furcigerum*, Abänderung mit verdoppelten Fortsätzen. „Dichotypische Zelle“.

Desmidiologie bilden vielleicht die einzige Ausnahme die Fälle abnormaler Zellteilung und abnormalen Wachstums bei der Gattung *Closterium*. Vertreter dieser Gattung haben fast immer die Zellen mehr oder weniger bogenartig gekrümmt. Bei der Mehrzahl der Arten kommt es nicht selten vor, dass sich die jüngere Zellhälfte zu der der älteren Hälfte entgegengesetzten Seite hin krümmt, so dass das ausgewachsene Individuum eine sigmoide Form hat (Fig. 35). Seltener ist die jüngere Zellhälfte nicht um 180° , sondern nur um 90° gedreht.

Die Ursachen dieser Erscheinung sind bisher unbekannt. Schon Borge (1896) hat jedoch festgestellt, dass solche sigmoide Individuen aus normalen Zellen bei der Teilung entstehen. Trotzdem werden noch heute manchmal solche unbeständige Abnormitäten als selbständige systematische Einheiten, meistens als „f. *sigmoideum* n.f.“ beschrieben. Solche Benennungen sind selbstverständlich laut des zitierten Art. 67 des Intern. Codes unzulässig und vermehren nur die Verzeichnisse der Synonyme. Ähnlich gekrümmte und gewundene Zellen sind auch bei *Pleurotaenium* unzulässig als „f. *sigmodeum*“ bezeichnet, weiter werden solche auch bei *Cosmarium* (Fig. 36) und *Tetmemorus* gefunden, und eine ähnliche Erscheinung kommt auch bei *Arthrodesmus* und *Staurastrum* vor („f. *alternans*“, „f. *tortum*“) etc.

Ökologisch bedingte Abänderungen, „Modificationen“, sind manchmal schwer von den Monstrositäten zu unterscheiden, und umgekehrt entstehen oft Monstrositäten infolge des Einflusses von besonders ungünstigen ökologischen Bedingungen; da gibt es keine genaue Grenze. Der Internationale Code verwirft zwar Namen der Taxa, welche auf Monstrositäten beruhen (Art. 67), macht jedoch keine Einwendungen gegen die Benennung anderer nichtständiger Abänderungen, auch wenn sie ökologisch bedingt sind. Den in diesem Aufsatz angeführten Ansichten zufolge sollen beide Sorten von Abänderungen konsequent für nichttaxonomisch gehalten werden.

Eine weitere Kategorie von nichtständigen Abänderungen können wir bei gewissen Arten der Gattung *Staurastrum* beobachten. Bei diesen stehen an jeder Ecke zweierlei Fortsätze: die Ecke selbst ist in einen Fortsatz verlängert, und oberhalb desselben steht noch ein apikaler Fortsatz, welcher aber auch verdoppelt sein kann. Ein Vertreter solcher Arten ist *Staurastrum furcigerum* Bréb. ex Arch., welche an jeder Ecke zwei übereinander stehende Fortsätze besitzt (Fig. 40 b). Schon im J. 1843 hat jedoch Ehrenberg eine sehr ähnliche Alge beschrieben, welche sich von jener nur dadurch unterscheidet, dass ihre oberen Fortsätze verdoppelt sind (Fig. 40 b'); sie wurde zuerst für eine selbständige Art ge-

halten, *St. eustephanum* (Ehrenb.) ex Ralfs, später von Nordstedt als „f. *eustephanum*“ der *St. furcigerum* zugeordnet. In diesem Falle können jedoch zwei Beweise geführt werden, dass es sich hier um keine selbständige Einheit (auch nicht um eine „forma“) handelt. Es werden auch dichotypische Zellen gefunden, bei welchen die eine Zelhälfte „*furcigerum*-ähnlich“, die zweite „*eustephanum*-ähnlich“ ist (Fig. 40 a—a'). Eine von den beiden Abänderungen kann sonach in die andere bei der vegetativen Zellteilung übergehen. Und noch weiter, in W. et G. S. West et N. Carters Monographie (1923, tab. 156 Fig. 8) ist eine Zygosporangie abgebildet, welche durch die Konjugation von einer „*furcigerum*-Zelle“ und einer „*eustephanum*-Zelle“ gebildet ist. Dies bedeutet, dass zwei morphologisch auffallend verschiedene Abänderungen in einem einzigen Klone erscheinen und miteinander auch kopulieren können, also nicht ständig und nach unseren obigen Behauptungen auch nicht taxonomisch sind: sie dürfen nicht als verschiedene Taxa (nicht einmal als formae) registriert werden, sondern müssen nach den nomenklatorischen Regeln unter dem einzigen gemeinsamen Namen vereinigt werden.

Ähnliche Ansichten vertreten auch Grönblad und Scott (1955) in einem Aufsatz, wo sie die morphologisch auffallend verschiedenen Zellen (Fig. 19 und 21), wie auch die dichotypischen Zellen (Fig. 20) unter einem Namen, *Staurastrum bibrachiatum* Reinsch vereinigt haben. Für die einzelnen nichtständigen Abänderungen haben sie den Ausdruck „typus“ in demselben Sinne benützt, für den hier „morpha“ oder „modificatio“ empfohlen wird. In diesem Falle ist jedoch die Sache nicht so klar wie in dem vorigen. Wie schon die Autoren selbst betont haben, sind unter den morphologisch ähnlichen Abänderungen mit nur vier Fortsätzen an der Zelle vielleicht zwei selbständige Taxa verborgen, das eine, *St. smithii* Teil., dessen Fortsatzanzahl sich nicht ändert, und das zweite, welches mittelst der dichotypischen Abänderungen in die morphae mit acht Fortsätzen übergeht; das letztere muss nur als eine modificatio oder morpha des *St. bibrachiatum* Reinsch bezeichnet werden. Diese Frage ist noch durch ein weiteres Studium zu klären.

Es gibt noch eine ganze Reihe von *Staurastrum*-Arten, die an ihren Ecken entweder eine einfache oder eine doppelte Besetzung haben, sonst aber sehr ähnliche bzw. identische Zellen aufweisen. Soweit man sie bisher für selbständige Taxa hält, wäre es erforderlich, sie einer Revision zu unterwerfen. Zu erwähnen sind namentlich *St. tohopekaligense*, *St. senarium*, *St. hantzschii*, *St. renardii*, *St. furcatum* var. *furcatum* und var. *subsenarium*, *St. laeve* var. *laeve* und var. *supernumerarium*, *St.*

monticulosum var. *monticulosum* und var. *groenlandicum*, *St. subavicula* und andere. Hier ist es nicht angebracht, ihre sehr verwickelte Systematik und Synonymik zu erläutern.

In neuerer Zeit werden auch Fälle angeführt, wo es innerhalb eines einzigen Klones einer Alge zu Änderungen kam, die für ständig gehalten werden und denen dann gewöhnlich der Charakter einer Mutation zuerkannt wird. Solche Abänderungen entstanden meistens infolge drastischer äusserer Einflüsse (Bestrahlung, chemische Stoffe, Wechsel der Ernährung, Zentrifugierung u.a.). Als Beispiel können unter den Desmidiaceen die physiologisch und morphologisch stark veränderten Klone der Gattung *Micrasterias* dienen, welche Kallio (1951, 1953, 1954) in Kulturen erzielt hat. Wenn es hier erweislich zur Entstehung einer neuen ständigen Abänderung käme (die Ansichten über die Ständigkeit der in Kulturen erzielten Abänderungen sind in der Literatur höchst verschieden), so würde für sie dasselbe gelten, was oben von den ständigen Abänderungen gesagt wurde.

Sämtliche bisher angeführten Beispiele von nichtständigen Abänderungen sind vom morphologischen Standpunkte aus sehr auffallend. Dieser Umstand darf uns selbstverständlich nicht irreführen, sie taxonomisch anders als die unauffälligen Abänderungen zu bewerten. Die Auffälligkeit irgendeines nichtständigen Merkmales darf kein Beweggrund dafür sein, es als taxonomisch wertvoll zu betrachten.

Die morphologisch unauffälligen Abänderungen in den Dimensionen, in der Zellform und Skulptur, in den Details der Bauart der Chromatophore usw. erscheinen natürlich weit häufiger als die auffälligen und bilden grosse Schwierigkeiten bei der Bewertung der Merkmale. Eventuelle ständige Abänderungen pflegen oft von den auffallenderen nichtständigen gänzlich verdeckt zu werden. In der Desmidiologie wird oft namentlich den kleinen Verschiedenheiten in den Dimensionen ein taxonomischer Wert unrechtmässigerweise zugeschrieben; verschiedene „var. *major*, *minor*, *longior*, *brevior*, *robustior*“ u.a. sind manchmal nur blosse nichttaxonomische Modifikationen.

VI. Facies

Als charakteristisches Beispiel von Schwierigkeiten, denen wir bei der Beurteilung von ständigen und nichtständigen Abänderungen vom taxonomischen Standpunkte aus begegnen, ist die „facies“ (Teilung 1950, 1952) an dieser Stelle ausführlicher zu erwähnen.

Die Mehrzahl der Desmidiaceen (Teilings „anguloradiate Gattungen“,

z.B. *Cosmarium*, *Euastrum*, *Micrasterias*, *Xanthidium*, *Staurastrum*, *Desmidium* und manche andere) besitzt die Fähigkeit, die Zahl der durch die Apikalachse der Zelle gedachten Symmetrieebenen zu ändern. Diese Erscheinung nennt Teilung (l.c.) „Radiation“. Über deren Ursachen ist bisher wenig bekannt; nach Versuchen von Kallio ist sie aber von dem Zellkerne stark beeinflusst.

Gewisse anguloradiatale Gattungen (*Cosmarium*, *Euastrum*, *Micrasterias*, *Xanthidium* u.a.) haben normal zwei solche Symmetrieebenen, d.h. ihre Zellen sind biradiat (Fig. 38). Manchmal, unter natürlichen Verhältnissen aber sehr selten, am häufigsten wohl noch in den arktischen oder alpinen Regionen, kommen doch bei diesen Gattungen Individuen vor, bei denen die Anzahl der Symmetrieebenen auf drei erhöht ist (Fig. 39). Ausnahmsweise wurden in Kulturen auch quadriradiatale Zellen hervorgebracht (Kallio 1951 bei *Micrasterias*), ja sogar uniradiatale Zellen (ibid.).

Bei anderen Gattungen, namentlich bei der Gattung *Staurastrum*, liegen die Verhältnisse etwas anders. Die Mehrzahl der Individuen hat hier polyradiatale Zellen, und Veränderungen in der Radiation kommen hier häufiger vor als in der erstgenannten Gruppe. Manchmal ist die Zahl der Radiationen auf zwei reduziert, manchmal wieder vermehrt. Bei *Staurastrum meriani* Reinsch sind z.B. 3- bis 11-radiatale Zellen bekannt.

Die einzelnen Abänderungen in bezug auf die Radiation hat Teilung (1952) als „facies“ bezeichnet. Teilung selbst hat zwar ursprünglich den speziellen Terminus nur für die von ihm neugebildete Gattung *Staurodesmus* (1948) in Anwendung gebracht, später aber (1950) mit vollem Recht für sämtliche „anguloradiatale“ Desmidiaceen empfohlen. Die Fähigkeit zur Bildung von Abänderungen in der Radiation ist für die Mehrzahl der Desmidiaceen so allgemein und charakteristisch, dass die Einführung dieses neuen Fachausdruckes „facies“ vollkommen begründet ist.

(Teilung 1954 unterscheidet sogar als eine separate Tribus die „anguloradiaten“ Gattungen im Gegensatz zu den „omniradiaten“. In der ersten Gruppe kommt die Radiation in der äusseren Zellform zum Vorschein, und die Chromatophoren sind „furförmig“; in der zweiten Gruppe ist der Querschnitt der Zellen genau kreisförmig, und die Chromatophoren sind „stellöid“. Die Anzahl der Chromatophorstrahlen schwankt natürlich auch bei den „omniradiaten“ Desmidiaceen, welche sonach auch eine gewisse, nur den Chromatophor betreffende Radiation aufweisen; die Anzahl der Längsleisten schwankt z.B. bei manchen Closterien ganz beträchtlich. Auf Grund der Unterschiede bei „anguloradia-

ten“ und „omniradiaten“ Desmidiaceen entwickelt Teiling weitgehende systematische und phylogenetische Schlüsse, die schwer annehmbar sind.)

Einzelne „facies“ verändern sich nicht selten von einer zur anderen im Rahmen eines einzigen Klones während der vegetativen Zellteilung, wie dies die nicht selten vorkommenden dichotypischen Individuen (hier von Teiling als „Janus-Formen“ benannt) zeigen; bei diesen weist die eine Zellhälfte eine andere Anzahl von Symmetrieebenen als die zweite auf. Es wurde auch die Kopulation von zwei verschiedenen facies beobachtet. In diesen Fällen handelt es sich offensichtlich um nicht-ständige Abänderungen, auf die sich alles das bezieht, was oben darüber gesagt wurde.

So sehr wir auch subjektiv von der Richtigkeit der unten gebrachten Ausführungen überzeugt sind, so liegt uns fern zu behaupten, dass sie als die einzig gültigen anzusehen seien, umsomehr da sie auf noch nicht genügend aufgeklärte Umstände gegründet sind.

Einzelne Abänderungen in der Radiation sind nämlich offenbar taxonomisch nicht gleichwertig. Wie schon oben erwähnt, besteht bei den Gattungen *Cosmarium*, *Euastrum*, *Micrasterias*, *Xanthidium* und manchen anderen ein absolutes Übergewicht an biradiaten facies, wogegen die triradiaten eine weit seltenere Ausnahme bilden und die quadri-radiaten resp. uniradiaten nur durch künstliche Eingriffe in der Kultur hervorgebracht sind. Das bedeutet, dass die in der Natur neugebildete polyradiate facies entweder nichtständig ist und rasch in die frühere biradiate zurückkehrt, oder zwar ständig, aber unter den gegebenen Umständen eines längeren Lebens unfähig ist und bald abstirbt. Die biradiaten facies sind hier also offensichtlich entweder beständiger oder lebensfähiger als die triradiaten.

Noch verworrener sind die Verhältnisse bei der Gattung *Staurastrum*. Hier kommt es viel häufiger zur Bildung verschiedener facies und diese weisen oft einen dauerhafteren Charakter auf. Nichtdestoweniger kann auch hier bei einer Mehrzahl der Arten eine bestimmte Anzahl von Radiationen (meist 2 oder 3) als „normaler Grundzustand“ gelten. So sind z.B. *Staurastrum bibrachiatum* Reinsch (Fig. 19—21) und *St. bicornae* Hauptfl. konstant 2-radiat, *St. manfeldtii* Delp. überwiegend 3-radiat, *St. quadrangulare* Bréb. ex Ralfs und *St. brasiliense* Lund. var. *brasiliense* überwiegend 4-radiat, *St. brasiliense* var. *lundellii* W. et G. S. West meistens 5-radiat etc. Abweichungen von dieser „normalen“ Zahl, falls sie überhaupt erscheinen, sind hier deutlich seltener. Dagegen kommen auch Fälle vor, wo zwei oder mehrere facies „Normalzustand“ zu

sein scheinen, z.B. die 4- und 3-radiaten facies bei *St. gracile* Ralfs und *St. paradoxum* Meyen ex Ralfs, beide sensu G. M. Smith (1924).

Man gewinnt somit deutlich den Eindruck, dass, insofern es sich um die Radiation handelt, einerseits mehr oder weniger stabilisierte und wohl auch erblich fixierte, andererseits vorübergehende und unbeständige Abweichungen vorkommen. Erweist sich diese Vermutung als berechtigt, so halten wir es nicht für richtig, für beide Fälle denselben Terminus „facies“ zu gebrauchen. Facies sollte nur für die in der Radiation nichtständigen und folglich nichttaxonomischen Abänderungen vorbehalten bleiben. Dagegen sollte für die in der Radiation ständigen, taxonomischen Kategorien irgendeiner von den taxonomischen Termini angewandt werden, z.B. „varietas“ oder „forma“. Demnach sollten auch für die Abänderungen in der Radiation die gleichen Regeln gelten, wie für irgendwelche andere, sowohl ständige als auch unbeständige Abänderungen.

Ein praktisches Beispiel kann die in Fig. 39 abgebildete triradiatale Abänderung der Art *Xanthidium antilopaeum* (Bréb.) ex Kütz. bieten. Wenn man sie für eine ständige Abänderung hält, soll man sie entweder „var. *triquetrum* Lund.“ oder auch „f. *triquetrum* (Lund.) comb. nova“ benennen. Wenn wir aber erwiesen haben, oder — weil ein Beweis im gegenwärtigen Stadium in der Praxis kaum durchführbar ist — wenn wir aus Erfahrung behaupten können, dass sie nichtständig ist, so müssen wir einen nichttaxonomischen Terminus anwenden; wir können sie mit den Worten „facies e vertice triradiata“ oder „triradiatale Facies“, oder auch „fac. triradiata“, eventuell auch — wie Teiling der Kürze halber empfiehlt — „fac. 3“ beschreiben, keineswegs aber als „var. *triquetrum*“ oder „fac. *triquetrum*“ oder sogar „fac. *triquetrum* (Lund.) comb. nova“.

Taxonomische Termini sind unserer Ansicht nach auch in dem Falle anzuwenden, falls vielleicht überhaupt kein anderer Unterschied als eine als ständig erwiesene Abweichung in der Radiation existieren sollte. Es scheint aber in Wirklichkeit als wenig wahrscheinlich, dass sich zwei stabilisierte Einheiten, zwei Taxa, nur in einem einzigen Merkmale unterscheiden sollten. Meistens handelt es sich bei den Taxa um einen ganzen Komplex von konstanten Merkmalen, wobei mitunter manche kaum deutlich sein können.

Bei der von Teiling (1948) gebildeten Gattung *Staurodesmus* sind die erkennbaren morphologischen Merkmale nur von verhältnismässig geringer Anzahl, was dazu verleiten kann, einer markanten Abänderung

in der Radiation eine übermässige Bedeutung beizulegen. Deutlicher liegen die Verhältnisse bei der Gattung *Staurastrum*. Als Beispiel können wir *St. brasiliense* Nordst. 1870 nennen. Diese Art ist in der in den Tropen verbreiteten var. *brasiliense* meistens quadriradiat; eine 5-radiate Facies ist zwar von Nordstedt (l.c.) auch erwähnt worden, es kann sich aber hier um die ebenfalls tropische var. *porrectum* Borge handeln, die damals noch nicht beschrieben war. Dagegen ist die in Europa vorkommende var. *lundellii* W. et G. S. West (1896) überwiegend 5-radiat. Beide Varietäten kann man jedoch laut W. und G. S. West und N. Carter (1923) auch auf Grund anderer Merkmale unterscheiden. Sie können somit vollberechtigt als zwei verschiedene Varietäten, und nicht nur als blosse Facies, angesehen werden.

Ohne Zweifel müssen wir uns in zahlreichen Fällen noch lange mit mehr oder weniger begründeten Annahmen und Vermutungen begnügen, da es ebenso schwer fällt, ständige und nichtständige Abänderungen in der Radiation zu unterscheiden, wie andere ständige und unbeständige Abänderungen. Dieser Schwierigkeit begegnen wir jedoch bei Fragen, die taxonomische und nichttaxonomische Begriffe betreffen, ganz allgemein: wie bereits gesagt wurde, können wir mit den Versuchen, ein vernünftiges und annehmbares System aufzustellen, nicht solange warten, bis sämtliche Zweifel beseitigt sein werden.

Es ist nicht zu erwarten, dass sofort Einigkeit darüber erzielt werden wird, in welcher Weise geringfügige Abänderungen beurteilt werden sollen. Noch lange wird eine grosse Zahl von Autoren geneigt sein, sowohl jede unbedeutende als auch nichtständige Abänderung zu beschreiben; die Synonymenverzeichnisse werden noch lange anwachsen.

Es ist an der Zeit, einmal schon allen Ernstes darüber nachzudenken, wie übermässig kompliziert das System bereits geworden ist und wie wenigstens für die Zukunft derartigen Nachteilen zu begegnen wäre. Das System der Desmidiaceen ist in einigen Gruppen bereits dicht an die Grenze des Unverständlichen herangekommen. Es ist unsere Hoffnung, dass die obangeführten Grundsätze, falls sie angenommen und befolgt werden, einen wesentlichen Schritt zur Verbesserung des chaotischen Zustandes der gegenwärtigen Algensystematik bedeuten können. Das Festhalten an dem bisherigen Verfahren wird in Zukunft, wie wir befürchten, dazu führen, dass sich Paschers (1925, p. 100) Ansichten über die ebenso verwickelte Systematik der Gattung *Tribonema* geltend machen: „Hier kann nur reiner Tisch gemacht werden . . .“

On the Taxonomy of Desmidiaceae

English Summary

The general conception of species and infraspecific taxa in the Desmidiaceae is at present very obscure. In most cases the extent of variability of a given taxon is unknown. Occasionally, however, evidence is obtained showing that the variability is essentially greater than generally has been thought possible. Thus it is always necessary to inquire into the total variability, even when we have to do with a seemingly narrowly limited form. So it is necessary in doubtful cases to allow a somewhat broader conception of the taxon, especially of the "species". This must not, however, be exaggerated in *absurdum* so that we get what are called "Sammelarten", large heterogeneous species which include elements with little relation to each other. Such species as *Staurostrum polymorphum*, *St. gracile*, and *Arthrodesmus incus* with its varieties, are very awkward in practical work, giving rise to much trouble. At present, when the limits of the taxa are not defined exactly, smaller modifications may be annotated by the use of the special terms proposed below.

In order to avoid a continually increasing number of names and synonyms, and thus to avoid an obscurity of the whole system, a proposal is made as to certain limitations in the International Code of Botanical Nomenclature. First and foremost a strict separation of taxonomic and non-taxonomic variations should be kept. The conception of a taxon should be limited in such a way that only constant hereditary variations should be considered taxonomic units. Such a separation is not indicated or suggested anywhere in the Code (1956).

As to the taxonomic groups, only those mentioned in Art. 4 of the Code should be used. In the Algae, especially Desmids, the use of only the following terms is recommended: *species*, *varietas*, *forma*, and only in exceptional cases *subspecies*. It is evident that *forma* is to be treated as a taxonomic term and not to be applied (as in older times often was the practice) to non-taxonomic groups. Theoretically there is no reason against making every slight variation a taxonomic category and thus giving to it a taxonomic epithet. But in order to keep a somewhat clear summary of the system it must in practice be limited to the most essential cases, i.e., when there is in question a sufficiently important variation. The judgement of the importance of the variations must, however, depend on the skill and experience of the author.

The hereditarily not stabilized and thus inconstant, temporary, and retrogressive variations are non-taxonomic. Such products of variation must not be designated by means of taxonomic terms (e.g., *forma*). The present authors recommend for use in such cases where it seems necessary to have a special "name" the term "modification" (*modificatio*), — abbreviated "mod." — while the Czechoslovakian phycologists propose such terms as "*morpha*", "*ekomorpha*", "*status*". A special term, "*facies*", is, according to Teiling, to be used for the variation in radiation of desmids, this also being non-taxonomic.

A non-taxonomic term, with a description of the variation in question, may be joined with the epithet of the species, or of the particular infraspecific rank of the species in which it occurs. The differing modification should not be given an epithet in the nomenclatural sense, and no author's name is to follow.

The description is not to be understood as a diagnosis. If a Latin or Greek adjective is used its gender should not necessarily agree with that of the genus, but with that of the words "*modificatio*", "*morpha*", "*facies*", etc., these three being feminine.

The question as to the use of the term "*facies*" seems sometimes to be more obscure. There are "*facies*" which certainly are non-taxonomic and non-hereditary, (such as fac. 2 and fac. 3 found in the same filament of *Sphaerosma granulatum*, communicated by Růžička in litt.). Also among the *Staurostrum* it is not unusual to find individuals in which the two semicells are not of the same degree of radiation, and belong to different *facies*. On the other hand there seem to be a number of constant "*facies*" which then should be marked as taxonomic categories, varieties.

In the present state of our knowledge it is sometimes very difficult, — sometimes, indeed, impossible — to know whether a taxonomic or non-taxonomic character is involved. There must remain a degree of uncertainty as to the real nature of such variations. In such cases we are compelled to rely upon mere guesses and suppositions. This is, however, no reason why we should not try to use the nomenclatural terms logically and build up a system that corresponds with our current knowledge. Otherwise there is imminent danger that the whole system will become monstrously swollen and quite confused.

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The Morphology, Embryology and Systematic Position of *Elytraria acaulis* (Linn. f.) Lindau

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Lindau (1895) erected four sub-families under the family Acanthaceae: Nelsonioideae, Mendoncioideae, Thunbergioideae and Acanthoideae. Van Tieghem (1908) included the first three sub-families under a separate family Thunbergiaceae. Bhaduri (1944) doubted the validity of the sub-family Nelsonioideae as its pollen grains are not distinctive and resemble those of *Acanthus* and *Crossandra* (Acanthoideae). Recently, Bremekamp (1953) has transferred it to the Scrophulariaceae.

Concerning previous work, since the publication of Schnarf's (1931) "Vergleichende Embryologie der Angiospermen", wherein the earlier literature has been reviewed, Mauritzon (1934) has published a detailed account of endosperm development in several genera. He pointed out that the most interesting feature in the family is the Cellular type of endosperm but the 'endosperm proper' is the result of free nuclear divisions followed by wall formation in the central chamber. Rangaswamy (1941) studied the cytomorphology of *Asteracantha spinosa* and Rao (1953) has dealt with the floral anatomy of several genera.

More recently, the female gametophyte of *Elytraria acaulis*, *Barleria prionitis* and *Acanthus ilicifolius*, and endosperm and embryo development in *B. prionitis* have been worked out by Phatak & Ambegaokar (1955, 1956); the embryology of *Dipteracanthus patulus* by Maheshwari & Negi (1955); development of the endosperm and embryo in *Peristrophe*, *Adhatoda* and *Barleria* by Mohan Ram (1956); microsporogenesis in *Justicia betonica*, *Barleria prionitis* and *Ruellia tuberosa* by Narayanan (1956); pollen morphology of Tubiflorae by Natarajan (1957); life history of *Justicia simplex* by Mohan Ram & Sehgal (1958); and the endosperm of *Eranthemum nervosum* by Mohan Ram (1959).

Elytraria (Nelsonioideae), a common local plant, was taken up for a detailed study with a view to determine if the embryological data could throw some light on its systematic position.

Material and Methods

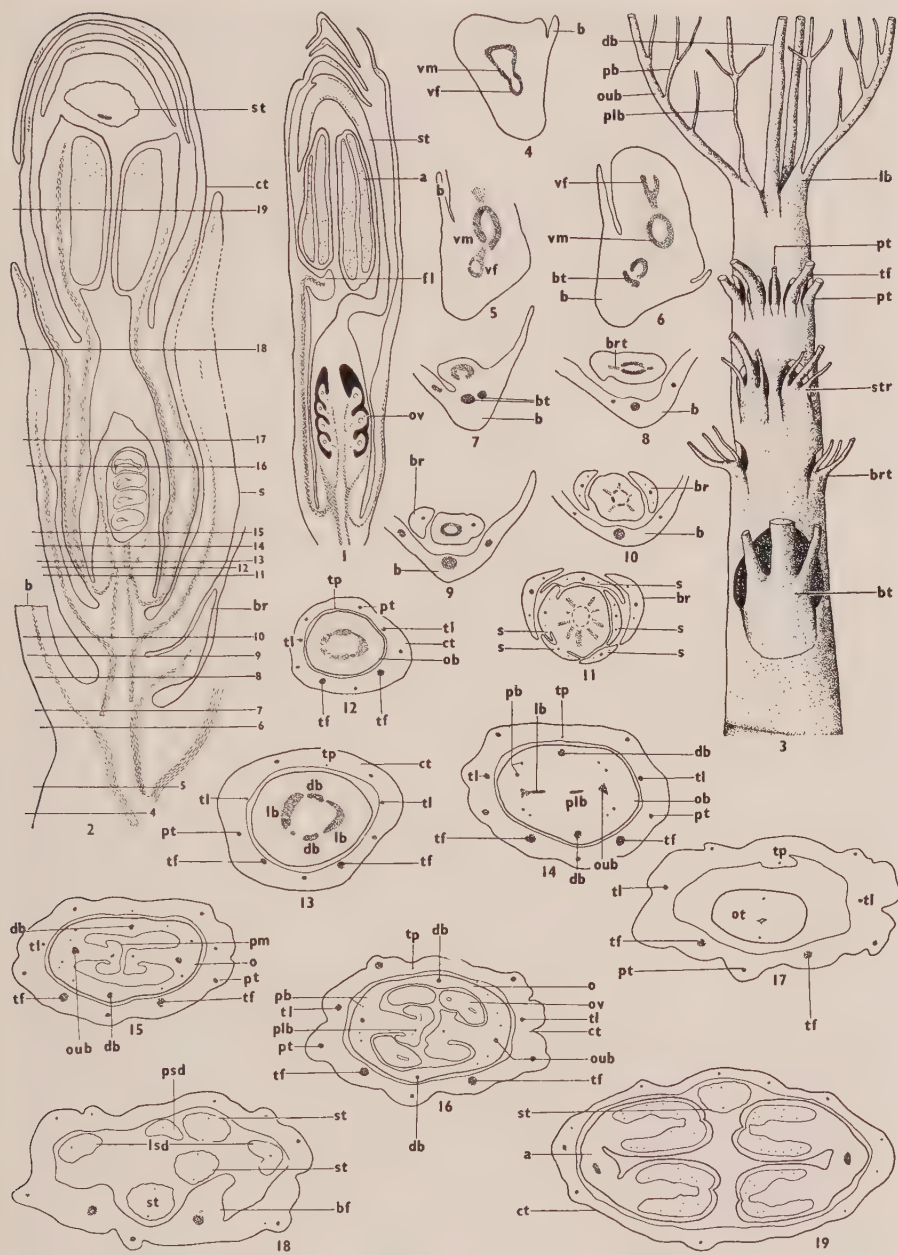
The material was mostly collected from the Delhi Ridge during August-September, 1954, and fixed in formalin-acetic-alcohol. The bracts, bracteoles and calyx were removed from the buds to facilitate infiltration. The ovules, due to their peculiar orientation, had to be sectioned individually for obtaining median sections.

Customary methods of dehydration and imbedding were followed. Some material was also processed in the tertiary butyl-alcohol series to prevent hardening. Sections were cut 6 to 15 microns thick, stained in iron-haematoxylin and counterstained with a dilute solution of alcoholic fast-green. For tracing the vascular supply in the floral parts, crystal-violet and erythrosin proved superior.

External Morphology

Several flowering scapes, each terminating in one, or occasionally two to three spikes, arise from the rosette of leaves and bear alternating scales. The scarious and spathulate bracts are very conspicuous but the

Figs. 1—19. — Bract, bracteole and calyx have not been shown in Figs. 1, 11—19. Of the five petal traces, only one has been labelled in Figs. 12—17 (*a*, anther lobe; *b*, bract; *bf*, base of fertile stamen; *br*, bracteole; *brt*, bracteole trace; *bt*, bract trace; *ct*, corolla tube; *db*, dorsal bundle; *fl*, filament of fertile stamen; *lb*, lateral bundle; *lsd*, lateral staminode; *o*, ovary; *ob*, base of ovary; *ot*, apex of ovary; *oub*, outer bundle; *ov*, ovule; *pb*, peripheral bundles; *plb*, placental bundle; *pm*, placenta; *psd*, posterior staminode; *pt*, petal trace; *s*, sepal; *st*, style; *str*, sepal trace; *tf*, trace of fertile stamen; *tl*, trace of lateral, *tp*, of posterior staminode; *vf*, vascular cylinder of flower; *vm*, vascular cylinder of inflorescence axis). Figs. 1, 2. Longisections of flower buds, at right angles to each other, showing vasculature; note the position of style. Levels of transverse sections represented in Figs. 3—18 are indicated in Fig. 2. $\times 24$. Fig. 3. Diagrammatic representation of the vascular skeleton in the basal portion of the flower, approximately between the levels marked 4 and 15 in Fig. 2. $\times 86$. Figs. 4, 5. Delimitation of vascular cylinder of the flower (*vf*) from the stele of the inflorescence axis (*vm*). $\times 40$. Figs. 6, 7. Origin and division of bract trace into three bundles. $\times 40$. Figs. 8, 9. Origin of bracteole traces, one of the bracteoles has separated in the latter figure. $\times 40$. Fig. 10. Origin of five calyx traces; each bracteole shows three bundles. $\times 40$. Fig. 11. Origin of stamen and petal traces; the trace to the posterior staminode is very feeble. $\times 40$. Figs. 12, 13. Basal region of ovary showing the origin of two dorsal (*db*) and two lateral (*lb*) bundles; in Fig. 13 one of the peripheral bundles has also been demarcated. $\times 40$. Fig. 14. Lateral bundles have formed the inner placental bundles (*plb*) and the outer bundles (*oub*); the number of peripheral bundles (*pb*) has increased. $\times 40$. Figs. 15, 16. Origin of ovules and orientation of placental bundles. $\times 40$. Fig. 17. T.s. ovary near the base of the style, the latter shows two dorsal bundles; the posterior staminode is also distinguishable. $\times 40$. Fig. 18. The three staminodes can be distinguished from the two fertile stamens, three sections of the style are due to its bent disposition (see Fig. 1). $\times 40$. Fig. 19. Upper part of flower showing two anthers and the style; the petal traces have divided in Figs. 18 and 19. $\times 40$.



Figs. 1—19.

two bracteoles are small. The bracts, bracteoles and sepals have a hairy margin.

The development of the floral organs is centripetal. The flowers are penatamerous and typically acanthaceous with one of the calyx lobes much bigger and two fertile stamens (Fig. 19). The bicarpellary, syncarpous gynoecium has a unilocular ovary which contains two rows of eight to ten ovules on parietal placentae. The style passes along the posterior side of the flower (Fig. 19) and ends in two laterally expanded unequal stigmas. The fruit is an ellipsoidal capsule with brown rounded seeds. It dehisces by breaking along the ventral sutures and the seeds are thrown out explosively.

Floral Anatomy

The vascular organization of the flower is shown in Figs. 1 to 19. A bract trace originates from the anterior side of the stele (Fig. 6) and is followed by the traces to the two lateral bracteoles which arise one after the other (Figs. 8—10). The stele of the floral axis now appears pentagonal and five sepal traces, one from each corner, become distinguishable (Fig. 10). Each of the bract, bracteole and sepal traces divides into three bundles before entering the respective organs (Figs. 7—11).

The five traces to the petals and another five to the stamens arise almost at the same level (Fig. 11) and dip downwards before entering the petals and stamens (Figs. 1, 2). Two of the staminal traces enter the fertile stamens while the remaining three supply the staminodes. The trace to the posterior staminode is feebly developed. Whereas the traces to the corolla divide in the petals, the staminal traces remain unbranched (Figs. 17, 18).

At the base of the gynoecium, the vascular cylinder splits up into four bundles — two smaller ones in the anteroposterior plane and two larger ones situated laterally (Figs. 12, 13). Each of the former occupies a median position in the corresponding carpel (Figs. 14, 15). Apparently, these are the dorsal bundles of the two carpels which continue unbranched into the style (Fig. 17) and the stigma (Fig. 2).

The lateral bundles divide in the meantime, and the inner trace enters the placental region of the corresponding side and supplies the ovules (Figs. 14, 16). It appears that the placental strand is formed by the fusion of the two ventral bundles belonging to different carpels. The outer trace gives off a few small peripheral bundles which enter the ovary wall (Figs. 15, 16). The position of the outer bundles on the septal

radii indicates that they may be the fusion products of two secondary marginal veins or septal strands.

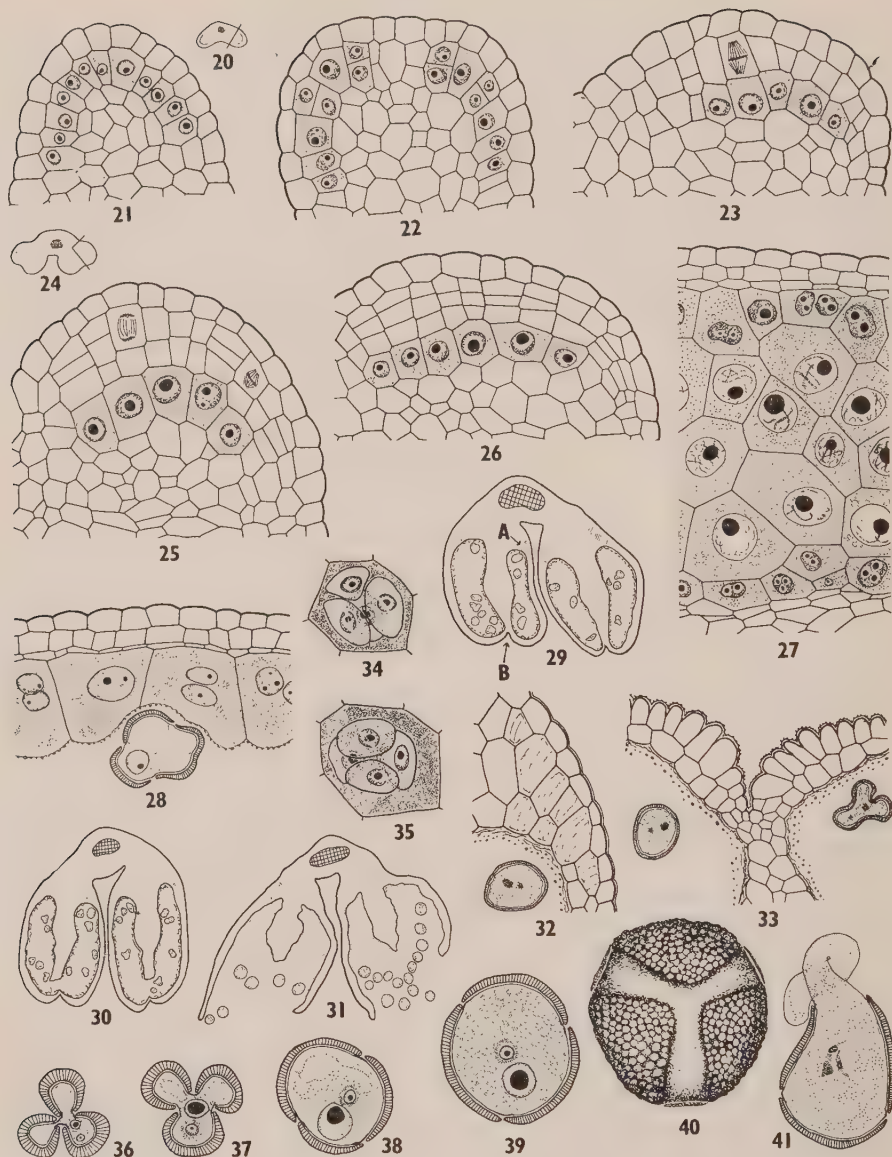
Figure 3 represents a reconstruction of the vascular skeleton in the basal portion of the flower between the levels marked 4 and 15 in Fig. 2.

According to Puri (1952), the placentation is parietal, if (a) the ovary is unilocular, (b) the placenta receives its supply from the ventral bundles of two different carpels, and (c) the orientation of the ventral (=placental in the present case) bundles is normal, i.e. they are not reversed. In *Elytraria acaulis* all the three conditions are attained. The placental bundles represent the fused ventral bundles of two different carpels, the ovary is unilocular (Figs. 15, 16) and the orientation of the placental bundles is normal. The placentation should, therefore, be considered as parietal and not axile as generally assumed for the family Acanthaceae.

Microsporangium

The young anther is two-lobed (Fig. 20) and there is a single layer of hypodermal archesporial cells in each lobe (Fig. 21). Due to sterilization of some of the medianly placed archesporial cells (Fig. 22), four groups are delimited and by this time the anther too becomes four-lobed (Fig. 24). As the microsporangia enlarge, they bend against the connective.

The archesporial cells divide periclinally (Figs. 22) to form the primary parietal layer and the primary sporogenous layer. Figures 23 to 26 show the progressive differentiation of the endothecium, middle layer, and the glandular tapetum from the primary parietal layer. In a mature anther, the outer tangential walls of the epidermal cells become somewhat papillate (Fig. 33). The cells of the endothecium elongate radially and fibrous thickenings appear only in small patches at the base of the microsporangia (Figs. 29—32). In *Dipteracanthus patulus* (Maheshwari & Negi 1955), the endothecium shows normal thickenings while in *Justicia betonica*, *Barleria prionitis* and *Ruellia tuberosa* (Narayanan, 1956) they are altogether absent. The middle layer is ephemeral and becomes flattened even before the reduction divisions have commenced (Fig. 27). The tapetal cells are at first uninucleate but due to mitotic divisions they become two to four-nucleate; subsequently the nuclei fuse (Figs. 27, 28). The epidermal and endothecial cells contain starch; and the so-called 'Ubisch' granules appear on the inner tangential walls of the tapetum (Fig. 28). The latter disorganises during the maturation of the pollen grains (Figs. 32, 33).



Figs. 20—41. — Figs. 20, 24. T.s. young anthers at two and four-lobed stages. $\times 34$. Fig. 21. Enlargement of the marked lobe from Fig. 20 to show the archesporium. $\times 665$. Fig. 22. Same, advanced stage. $\times 665$. Figs. 23, 25, 26. Anther lobes showing origin of wall layers; Fig. 25 is an enlargement of the marked portion in Fig. 24. $\times 665$. Fig. 27. Part of an anther lobe (l.s.) after differentiation of the tapetum; microspore mother cells are in prophase. $\times 665$. Fig. 28. Anther wall at the uninucleate stage of pollen grains. $\times 665$. Figs. 29—31. Stages in dehiscence of the anther. $\times 34$. Figs. 32, 33. Enlargement of portions marked A and B respectively in Fig. 29. $\times 336$. Figs. 34, 35. Tetrahedral and decussate tetrads. $\times 665$. Figs. 36—39. Two-celled pollen grains. $\times 672$. Fig. 40. Polar view (superficial) of the exine. $\times 672$. Fig. 41. Germinated three-celled pollen grain from a dehiscent anther. $\times 672$.

At the two-celled stage of the pollen grains, the partition wall between the adjacent microsporangia collapses, so that they become confluent (Fig. 30). Dehiscence occurs due to the breaking down of the thin-walled cells at the junction of the pollen sacs (Figs. 31, 33).

Microsporogenesis and Male Gametophyte

After the differentiation of the wall layers, the primary sporogenous cells divide to produce a large number of microspore mother cells (Fig. 27). The reduction divisions are simultaneous and cytokinesis occurs by furrowing. The microspores may be arranged in a tetrahedral or decussate fashion (Figs. 34, 35).

The centrally situated microspore nucleus cuts off a generative cell adjacent to the wall but it soon moves up and comes to lie near the vegetative nucleus (Figs. 36—39). The pollen grains are shed at the two-celled stage and contain abundant starch (Fig. 39). Occasionally, they may germinate *in situ* and become three-celled (Fig. 41).

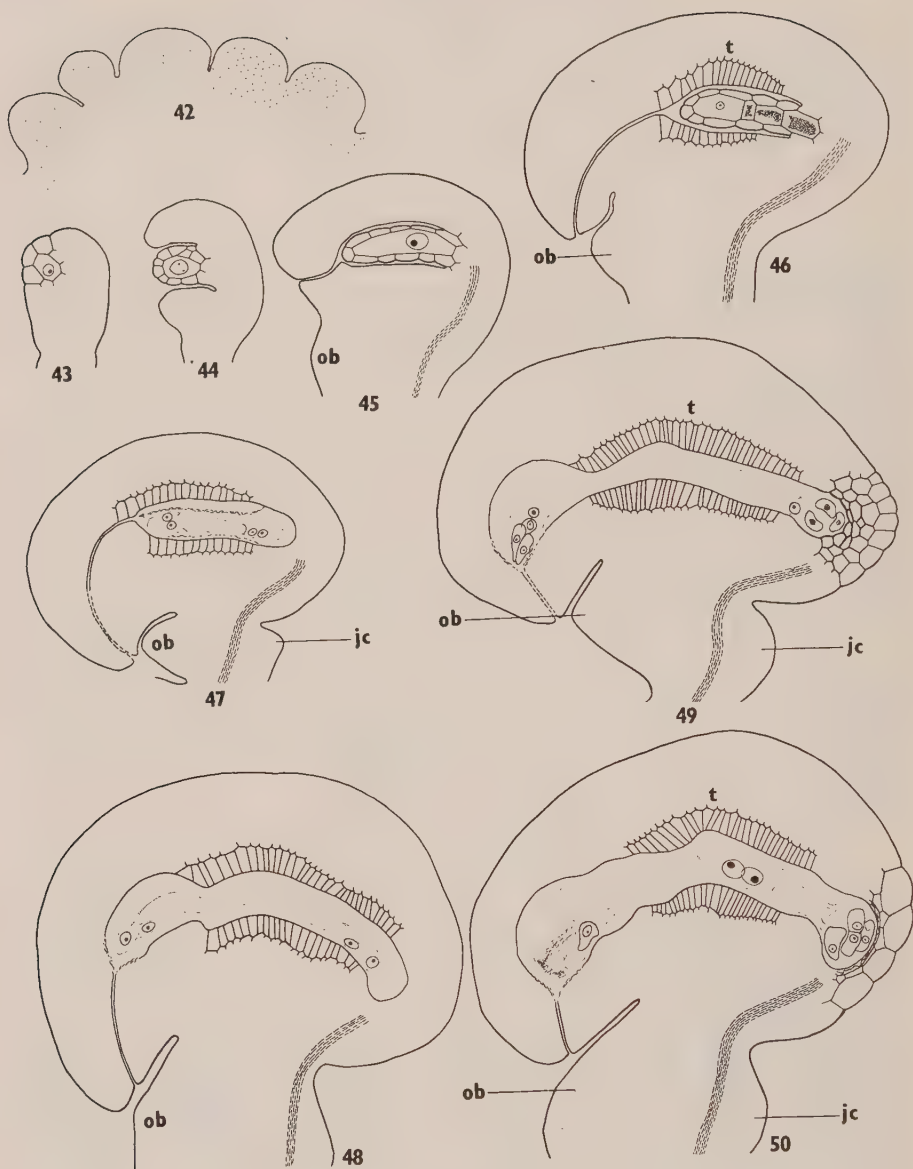
There are three germ pores in a young pollen grain, each situated in a deep longitudinal furrow (Fig. 36). As the pollen grain enlarges, it assumes a spherical shape (Figs. 36—38). This is accompanied by the thinning of the exine which shows prominent radial striations. The ripe pollen grains are isopolar, tricolporate (syncolpate) and symmetrical (Fig. 40).

Megasporangium

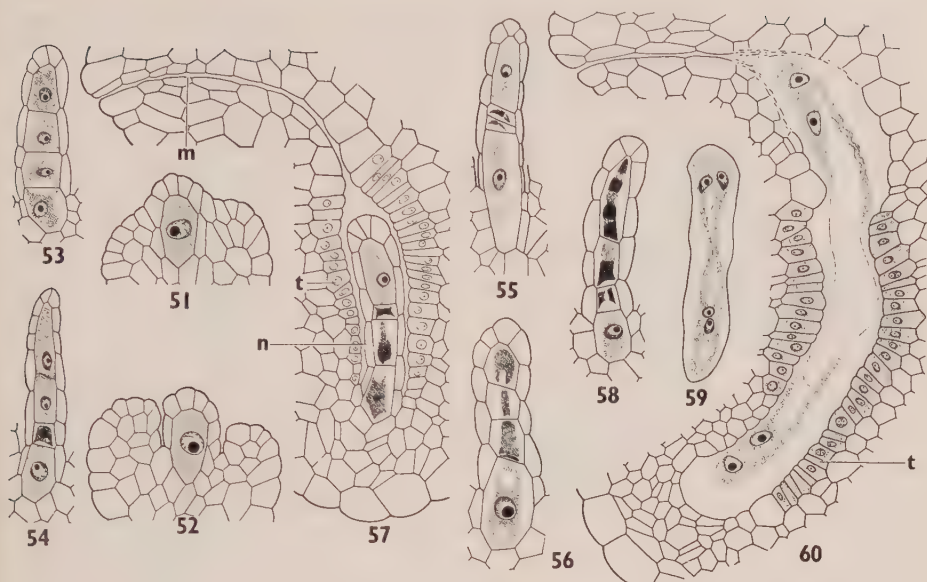
The ovules arise as tiny protuberances (Fig. 42), and the archesporial cell and the integument differentiate at about the same time (Fig. 43). With the elongation of the megaspore mother cell, the ovule shows a conspicuous curvature (Figs. 44, 45) and later becomes amphitropous (Figs. 46—50).

The nucellus, represented by a single layer of cells, degenerates early so that the embryo sac becomes directly surrounded by the integument (Figs. 46—50). At the megaspore tetrad stage, the inner epidermis of the integument differentiates into an endothelium (Fig. 46) which remains restricted to the middle portion of the mature gametophyte (Fig. 50). This feature is of common occurrence in the gamopetalous families but has so far not been reported in any other member of the Acanthaceae.

The funicular region adjacent to the micropyle swells to form the obturator and another outgrowth — the jaculator — is formed opposite



Figs. 42—50. — (*jc*, jaculator; *ob*, obturator; *t*, integumentary tapetum). Fig. 42. Ovular primordia. $\times 336$. Figs. 43—50. Progressive curvature and development of ovules from megaspore mother cell to mature embryo sac stages; note degeneration of the nucellus (Fig. 47) and origin of integumentary tapetum (endothelium), obturator and jaculator. $\times 336$.



Figs. 51—60. — (*m*, micropyle; *n*, nucellus; *t*, integumentary tapetum). Figs. 51, 52. L.s. upper part of ovules at megaspores mother cell stage. $\times 480$. Fig. 53. Linear tetrad. $\times 480$. Figs. 54—56. Degeneration of the non-functional megaspores. $\times 480$. Fig. 57. Enlarged micropylar megaspore with three lower ones degenerated. $\times 480$. Fig. 58. Abnormal tetrad. $\times 480$. Figs. 59, 60. Four-nucleate embryo sacs. $\times 480$.

to it (Figs. 46—50). An obturator has not been known before in this family. Bremekamp's (1953, 1955) report of the absence of a jaculator in *Elytraria* is incorrect.

Megasporogenesis

One or rarely two archesporial cells differentiate in the young ovule (Figs. 51, 52). The archesporial cell functions directly as the megaspore mother cell. Normally the tetrads are of the linear type (Figs. 53—57) and while the chalazal megaspore functions (Figs. 54—56), in one instance the micropylar megaspore had enlarged and the lower three cells had degenerated (Fig. 57). The arrangement in Fig. 58 may be due to twin tetrads or perhaps there is a single tetrad with the upper two megaspores showing abnormal structure.

Female Gametophyte

The functional megaspore undergoes three divisions leading to the formation of two, four and eight-nucleate gametophytes (Figs. 59—61).

Figure 61 represents an organised embryo sac showing the egg apparatus, lower and upper polar nuclei, and the three antipodal cells.

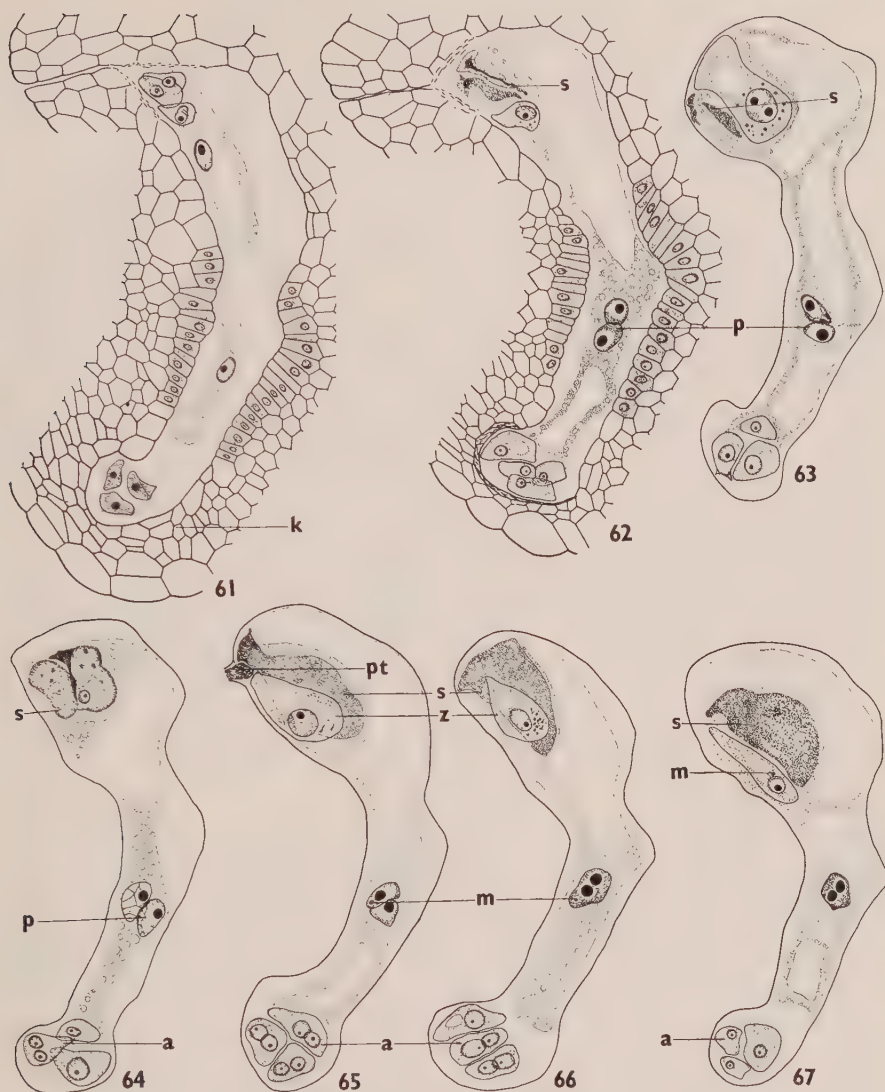
The synergids show signs of early degeneration (Figs. 62, 63), but one of them often persists and becomes hypertrophied after fertilization has taken place (Figs. 65—67). This takes a darker stain and remains distinguishable till the development of the endosperm has well advanced (Fig. 78). The egg contains prominent particles which stain like nucleoli with iron-haematoxylin (Figs. 62, 63, 65, 66). The polar nuclei migrate to the centre of the embryo sac where fusion takes place (Figs. 62—66).

The antipodal cells are richly cytoplasmic and one, two or all the three may become binucleate (Figs. 64—66). Some of the embryo sacs showed four antipodal cells (Figs. 62, 68). The latter remain healthy up to about the 10-celled stage of the central endosperm chamber. Supernumerary and persistent antipodal cells are rare in the Acanthaceae and have been reported only in two other genera: *Aphelandra* (Hartman, 1923) and *Barleria* (Mohan Ram, 1956; Phatak & Ambegaokar, 1956).

The four-nucleate embryo sac enlarges considerably (Figs. 59, 60). At this time the integumentary cells in the vicinity of the micropylar canal appear larger and are packed with starch grains. As the tip of the embryo sac elongates, these cells lose their contents and gradually disorganise leaving a bulbous space (Figs. 61, 62). The egg apparatus is situated in this region (Fig. 62).

At the eight-nucleate stage of the gametophyte, some of the cells at the chalazal end become thick-walled (Figs. 49, 61). The base of the embryo sac grows actively, crushes the surrounding tissue, and comes to lie against the ovular hypodermis close to the funicular vascular supply (Figs. 50, 62). The mature embryo sac has a characteristic curved appearance with swollen ends which seem to play a haustorial role (Figs. 61—67).

In *Dipteracanthus* (Maheshwari & Negi, 1955), the tip of the embryo sac protrudes into the micropyle while a prominent caecum develops at the antipodal end. Judging from the illustrations of Phatak & Ambegaokar (1955, Fig. 37), a chalazal caecum is formed in *Acanthus* although these authors seem to have missed it. In *Justicia simplex* (Mohan Ram & Sehgal, 1958) the tip of the embryo sac extends into a schizogenous cavity formed in the funicular region.



Figs. 61—67. — (a, antipodals; k, thick walled tissue; m, male gamete; p, polar nuclei; pt, pollen tube; s, synergid; z, zygote). Fig. 61. Eight-nucleate organized female gametophyte. $\times 480$. Figs. 62—64. Mature embryo sacs; both the synergids have degenerated, the polars are still free and there are four antipodal cells in Fig. 62, while in Fig. 64 one of the cells is binucleate. $\times 480$. Figs. 65, 66. Stages in triple fusion; all the antipodal cells are binucleate in Fig. 65 but only two in Fig. 66. $\times 480$. Fig. 67. Embryo sac showing primary endosperm nucleus; syngamy has not yet been completed. $\times 480$.

Fertilization

The pollen grains germinate on the stigma and the tubes travel through the solid style, pass over the funicular obturator, enter the micropyle and finally the embryo sac (Figs. 65, 68).

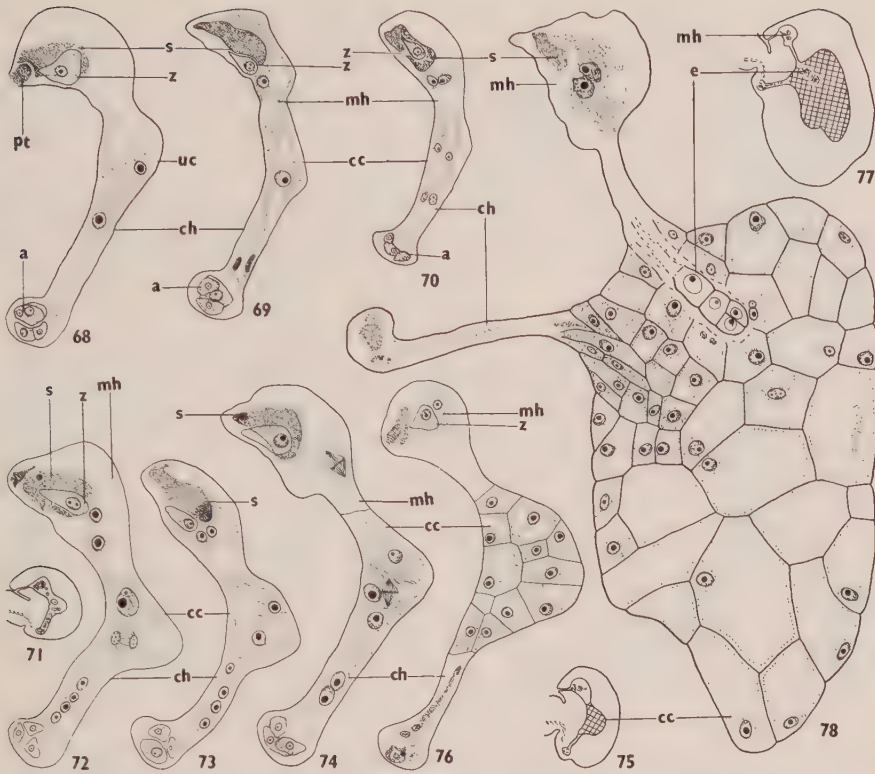
During triple fusion, the male gamete comes in contact with one polar nucleus (Fig. 65) before the latter fuses with the second polar (Fig. 66), but the fusion of the nucleoli is very much delayed (Fig. 67). The darkly staining granular particles present in the egg make it difficult to follow the fate of the second male gamete. However, in one embryo sac showing the primary endosperm nucleus, syngamy had not been completed and the male gamete was still discernible near the egg nucleus (Fig. 67). In *Dipteracanthus* (Maheshwari & Negi, 1955) also the process of double fertilization is similar to that of *Elytraria*. Mohan Ram & Sehgal (1958) observed normal triple fusion in *Justicia simplex*.

The remnants of the pollen tube persist till the maturation of the seed (Fig. 78). Persistent pollen tubes also occur in *Dipteracanthus* (Maheshwari & Negi, 1955) and many other plants (see Maheshwari, 1950; Maheshwari & Johri, 1950; Venkata Rao, 1952). Whether they have any haustorial role or merely represent the remnants of a dead structure is controversial. Maheshwari & Johri (1950) favour the latter view while Venkata Rao (1952) regards them as haustorial. As far as *Elytraria* is concerned, we are convinced that it does not have a haustorial function.

Endosperm

The first division of the primary endosperm nucleus is followed by the laying down of a membrane which separates the chalazal haustorium from the larger upper cell (Fig. 68). The latter divides again resulting in the formation of the micropylar haustorium and the central chamber (Fig. 69).

Micropylar haustorium — The micropylar haustorium shows two nuclei even at the two-celled stage of the central endosperm chamber (Figs. 70—73), but sometimes the nuclear division may be delayed (Fig. 74) or altogether omitted (Fig. 76). Occasionally, due to supernumerary divisions, the micropylar haustorium contains three, four (Figs. 79, 80) or even five nuclei. Rarely the division may be followed by a wall resulting in a two-celled condition (Fig. 81). In the beginning the nuclei have a regular outline but later they become irregular (Fig. 82), the size of the nucleolus also increases considerably and it



Figs. 68—78. — (*a*, antipodals; *cc*, central chamber; *ch*, chalazal haustorium; *e*, proembryo; *mh*, micropylar haustorium; *pt*, pollen tube; *s*, hypertrophied synergid; *uc*, upper cell; *z*, zygote). Fig. 68. First division of the primary endosperm nucleus resulting in a lower chalazal haustorium and an upper cell. $\times 288$. Fig. 69. The micropylar haustorium and the central chambers formed from the upper cell; the chalazal haustorium shows two degenerated nuclei. $\times 288$. Figs. 70, 72, 73. The central endosperm chamber is two-celled; the micropylar haustorium is two-nucleate whereas the chalazal haustorium is four-nucleate in Figs. 72 and 73 but only two-nucleate in Fig. 70. $\times 288$. Fig. 71. Index figure for Fig. 72. $\times 29$. Fig. 74. Nuclear division in micropylar haustorium, the central chamber is four-celled. $\times 288$. Figs. 75, 76. Asymmetrical growth of the central chamber; the micropylar haustorium is uninucleate while the chalazal haustorium has degenerated. Fig. 75 $\times 29$, Fig. 76 $\times 288$. Figs. 77, 78. Marked asymmetrical growth of central chamber; note the enlargement of the micropylar haustorium and degenerated chalazal haustorium. Fig. 77 $\times 29$, Fig. 78 $\times 288$.

may fragment. The haustorium contains dense and frothy cytoplasm which seems to aggregate in the upper portion giving a cap-like appearance (Figs. 82, 86).

The micropylar haustorium expands all round and consumes the adjacent integumentary cells. It persists in a healthy condition till the maturation of the seed (Fig. 86).

Chalazal haustorium — The single-celled chalazal haustorium is cut off medianly in the sub-terminal portion of the embryo sac and contains two to four nuclei (Figs. 69—74). It begins to degenerate as early as the four-celled stage of the central endosperm chamber and soon disorganizes completely (Figs. 75, 76).

In other members of this family also, the chalazal haustorium is one-celled but is cut off on the concave side of the embryo sac, except in *Crossandra* and *Acanthus* where it is cellular and median (Mauritzon, 1934).

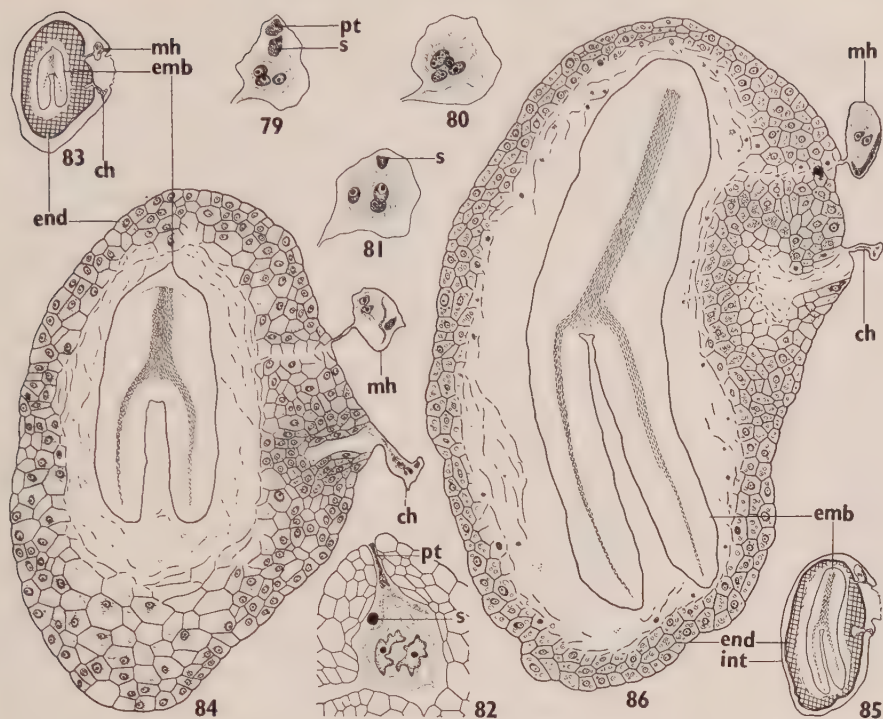
Central endosperm chamber — The first as well as the subsequent divisions in the central endosperm chamber are invariably followed by wall formation (Figs. 70—78). It expands rapidly, consumes the integument, and forms the bulk of the endosperm (Figs. 83—86). There is no free nuclear stage and a 'basal apparatus', as reported in other members of the Acanthaceae, is absent.

The growth of the central chamber is very asymmetrical (Figs. 76, 78) so that the micropylar and the chalazal haustoria shift from the terminal to a lateral position and come to lie close to each other. This unequal growth is mostly due to the enlargement of the basal cells of the central chamber (Fig. 78).

After the disorganization of the chalazal haustorium the adjacent cells of the central chamber elongate, become richly cytoplasmic and probably function as secondary haustoria (*see* Fig. 78). Subsequently, these cells also collapse (Figs. 83, 84) followed by the absorption of the adjoining cells (Figs. 85, 86). Mauritzon (1934) made similar observations in *Thunbergia*.

The endosperm consists of large, thin-walled and vacuolated cells containing prominent nuclei (Figs. 77, 78). During the maturation of the embryo oil globules appear in the cells close to the chalazal haustorium. Gradually, the entire endosperm becomes filled with fat globules which mask the nuclei (Fig. 108). The endosperm tissue around the embryo is always in a state of collapse (Figs. 84, 86).

A feature of special interest is the localized activity of some of the peripheral endosperm cells which form prominent ridges giving a ruminant appearance (Figs. 106—109). Such a condition is uncommon in the Acanthaceae but has been reported in many unrelated families like the Rubiaceae (Fagerlind, 1937); Myristicaceae, Thymelaeaceae (Mauritzon, 1939); Degeneriaceae (Swamy, 1949); Palmaceae (Venkata Rao, 1956) etc. The ruminant condition is usually due to the ingrowth of the integument. However, in *Psychotria* (Fagerlind, 1937), as in



Figs. 79—86. — (*ch*, chalazal haustorium; *emb*, embryo; *end*, endosperm; *int*, integument; *mh*, micropylar haustorium; *pt*, pollen tube; *s*, synergid). Figs. 79—81. Micropylar haustorium showing three and four nuclei; it is two-celled in Fig. 81. $\times 240$. Fig. 82. Upper part of ovule (l.s.); the micropylar haustorium contains two irregular nuclei, note remnants of the synergid and pollen tube. $\times 240$. Figs. 83, 85. Outline diagrams for Figs. 84 and 86. $\times 97$. Figs. 84, 86. Progressive stages in the development of endosperm and embryo; the micropylar haustorium is still quite healthy. $\times 108$.

Elytraria, it is due to unequal growth on the periphery of the endosperm. The phylogenetic significance of this feature is not clear.

According to Mauritzon (1934), the basal apparatus of the endosperm is present only in those species where the central chamber invades the integument rapidly and the chalazal haustorium contains four nuclei. He further states that when the central endosperm chamber becomes cellular at an early stage, the nuclear divisions in the chalazal haustorium may be omitted or delayed.

The present work on *Elytraria* fails to show any such correlation. Here the central endosperm chamber promptly invades the integument and the chalazal haustorium is also four-nucleate; nevertheless, the basal apparatus is absent. Moreover, the central chamber is cellular from the

very beginning and nuclear divisions in the chalazal haustorium also take place early. Maheshwari & Negi (1955) and Mohan Ram & Sehgal (1958) have reached a similar conclusion.

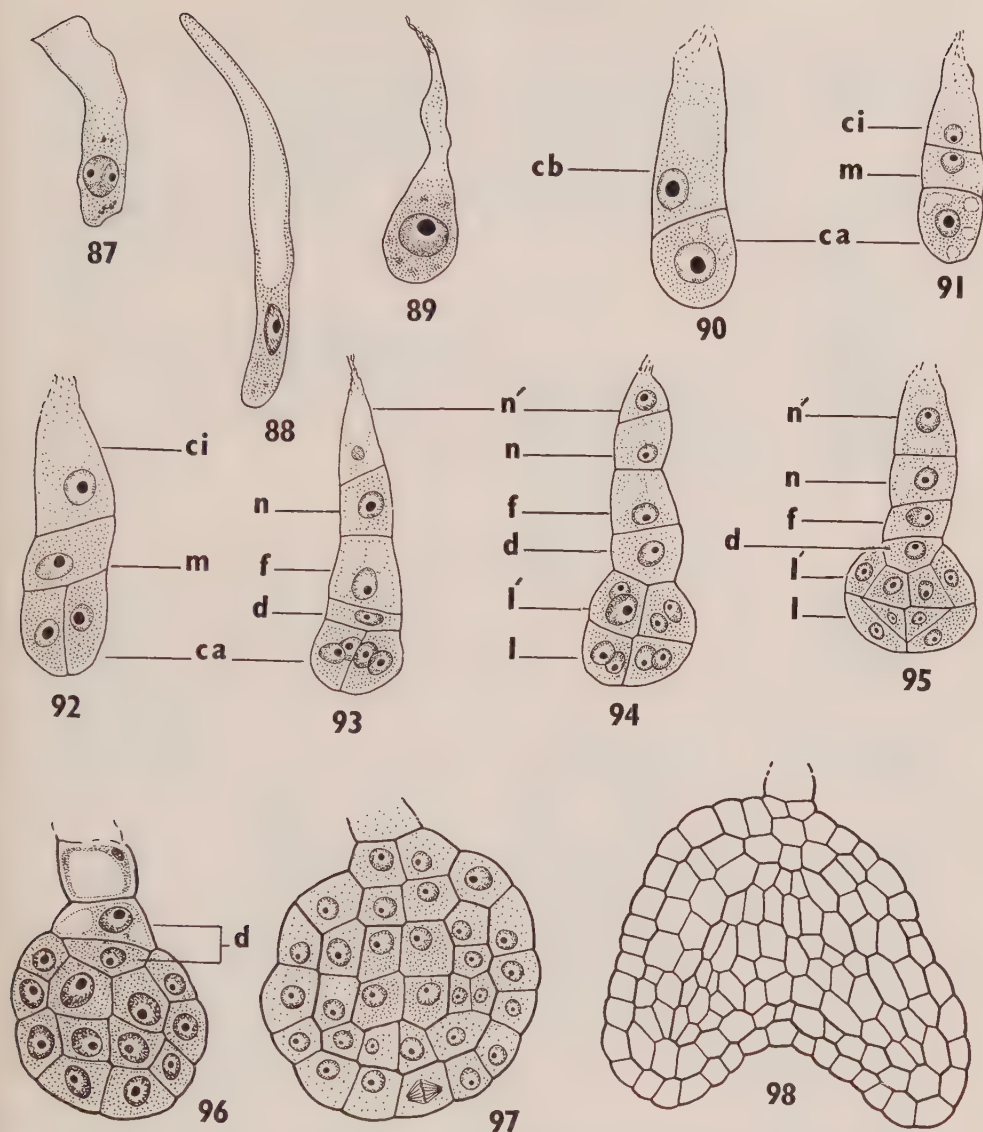
A unique feature of the central chamber is that in some genera (*Ruellia*, *Adhatoda* etc.) there is a free nuclear phase before the walls are laid down, and in others (*Crossandra*, *Acanthus*, *Elytraria* etc.) wall formation occurs from the very beginning. Mauritzon (1934) remarked: "... erachte ich es als am wahrscheinlichsten, dass Gattungen und Arten mit gut ausgebildetem Basalapparat und der damit meistens einhergehenden späten Zellenbildung als ursprünglich in der Familie aufzufassen sind, während die Schwächung des Basalapparates und die frühere Zellenbildung aus früheren Typen abgeleitet zu betrachten sind. ... erachte ich den oben angeführten Verlauf als den einzig möglichen und natürlichen. Wenn man den gut entwickelten Basalapparat als ursprünglich betrachtet, ist dessen langsame Schwächung leicht denkbar, während mir eine langsame und schrittweise Entstehung einer derartigen Bildung unmöglich erscheint".

After studying the pollen morphology of several genera of this family, Bhaduri (1944) came to the conclusion that *Crossandra* and *Acanthus* (both of which lack free nuclear divisions in the central chamber) should be considered as the basic types, and *Adhatoda* and *Ruellia* (where free nuclear divisions occur) as advanced.

In our opinion, the genera showing the free nuclear phase in the central chamber cannot be regarded as primitive since this feature is absent in the ancestral family Scrophulariaceae. It appears that the evolutionary trend from the free nuclear to the cellular condition, as proposed by Mauritzon (1934), should be reversed and the genera with a short free nuclear phase (*Barleria*), or those without it (*Acanthus*, *Elytraria*), should be regarded as primitive. The progressive origin of the free nuclear condition (in genera like *Ruellia*), conceived as impossible by Mauritzon, appears to be a more probable series. This is also supported by the views of Bhaduri (1944).

Embryogeny

The zygote elongates considerably (Figs. 87, 88) so that its tip containing the nucleus comes to lie in the central endosperm chamber. At the same time its basal portion shrinks and collapses (Fig. 89). The first division is transverse resulting in the tiers *cb* and *ca* (Fig. 90). Of these *cb* divides transversely forming the tiers *ci* and *m* (Fig. 91), which too



Figs. 87—98. — Figs. 87—96. Stages in development of the proembryo. $\times 950$. Figs. 97, 98. Globular and heart-shaped embryos. Fig. 97 $\times 950$, Fig. 98 $\times 480$.

undergo transverse divisions resulting in *d*, *f*, *n* and *n'* (Figs. 93—95). The tiers *f*, *n* and *n'* form the suspensor. Meanwhile, *ca* has twice divided longitudinally with the walls oriented at right angles to each other (Figs. 92, 93). This is the quadrant stage and a transverse divi-

sion leads to the formation of the octant with tiers *l* and *l'* (Fig. 94). Repeated periclinal and anticlinal divisions produce first the globular and then the heart-shaped embryo (Figs. 95—98). The tier *l* contributes to the cotyledons and the stem tip, and *l'* to the hypocotyl, plerome and periblem of the root. The first division of the tier *d* is transverse (Fig. 96) and its derivatives give rise to the root tip. Thus, the embryogeny corresponds to the *Lythrum*-variation of the *Onagrad* type (see Johnson, 1950).

The mature embryo is slightly curved and typically dicotyledonous (Fig. 86) with an elongated hypocotyl and disc-shaped cotyledons.

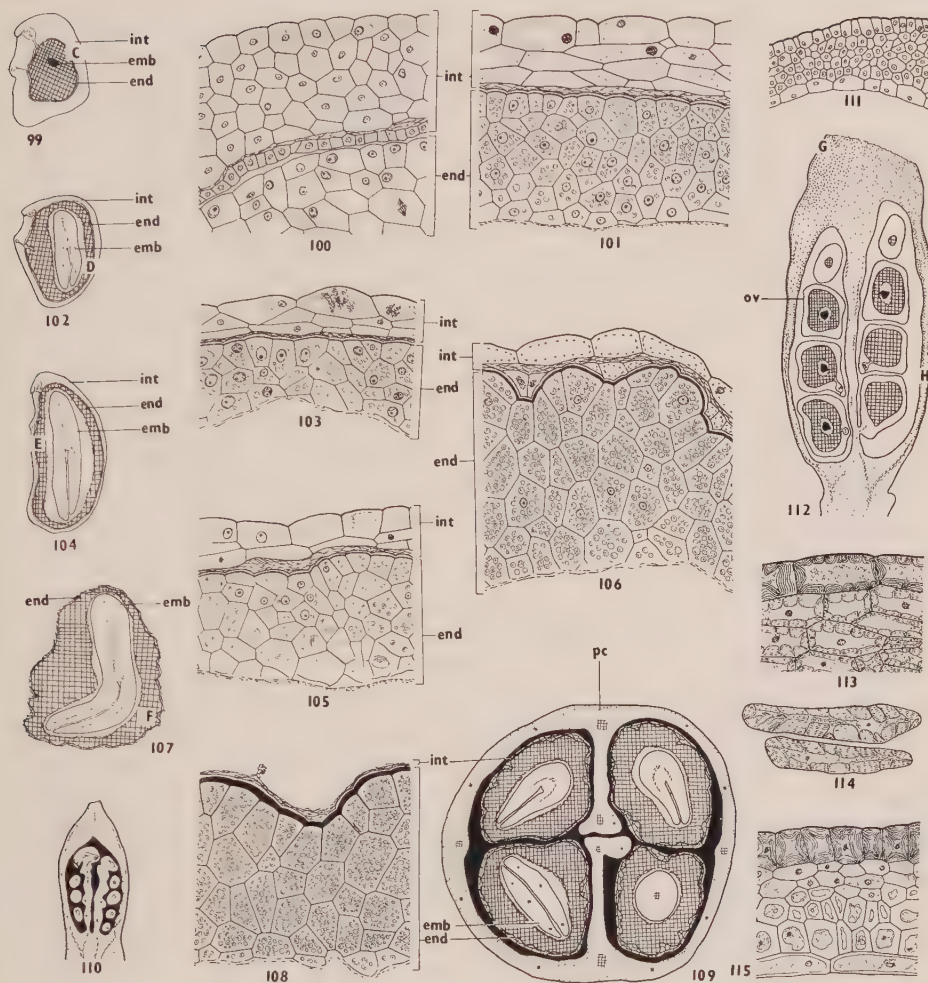
Elytraria differs from other members of the *Acanthaceae* in having a very short suspensor (see Mauritzon, 1934; Rangaswamy, 1941; Maheshwari & Negi, 1955; Mohan Ram, 1956).

Seed and Fruit

The young fruits are ellipsoidal enclosing white, round seeds arranged in four rows. The jaculator is small consisting of unthickened cells and seemingly plays no role in the dispersal of the seeds. This is in contrast to the situation in other members of the family where it is large and hook-shaped and helps in the expulsion of the seeds from the capsule.

Seed Coat — At the mature embryo sac stage, the integument consists of six to eight layers of parenchymatous cells and starch grains are present only in the micropylar and chalazal regions. During post-fertilization development the cells enlarge and starch accumulates in the entire integumentary tissue. The growth and expansion of the endosperm is accompanied by a progressive digestion of the integument until only about four layers survive (Figs. 99—101). At this time (Fig. 102), spiral and reticulate thickening appear in some of the epidermal cells (Fig. 103). Similar thickenings also develop in the hypodermal cells in the micropylar region. The absorption of the integument continues (Figs. 104, 105), but the tissue enclosed within the furrows of the ruminant endosperm (Fig. 106) persists for some time. Eventually epidermis also collapses and in the mature seed there is hardly any testa (see Figs. 107, 108). Figure 109 shows the disposition of the nearly mature seeds in the fruit.

Pericarp — The ovary wall comprises six to eight layers of parenchymatous cells containing scanty cytoplasm (Figs. 110, 111). During maturation of the seeds, the epidermal cells become highly sclerified leaving narrow, branched lumina (Figs. 112, 113, 115). However, the



Figs. 99—115. — (*emb*, embryo; *end*, endosperm; *int*, integument; *ov*, ovule; *pc*, pericarp). Figs. 99, 102, 104, 107. Outline diagrams for Figs. 100, 103, 105 and 108 respectively. $\times 24$. Figs. 100, 103, 105, 108. Enlargements of portions C, D, E and F marked in previous figures; note the gradual absorption of the testa and accumulation of fat globules in the endosperm tissue. $\times 240$. Figs. 101, 106. Intermediate stages between Figs. 100 and 103; and Figs. 105 and 108 respectively. $\times 240$. Fig. 109. T.s. fruit showing the disposition of seeds. $\times 24$. Fig. 110. L.s. ovary at the mature embryo sac stage. $\times 24$. Fig. 111. Pericarp (t.s.) at the stage shown in Fig. 110. $\times 240$. Fig. 112. L.s. fruit. $\times 24$. Figs. 113, 115. Pericarp (t.s.) from regions marked G (only a portion is shown) and H in Fig. 112. $\times 240$. Fig. 114. Isolated stone cells from the beak of fruit. $\times 240$.

degenerated remains of the nuclei and cytoplasm can still be recognised. The two to three sub-epidermal layers consist of thin-walled cells and are followed by another two to three layers of thick-walled cells (Fig. 115). The cells of the inner epidermis also acquire thick walls and elongate transversely. All the hypodermal layers are richly cytoplasmic and contain abundant starch (Fig. 115).

In the upper portion of the pericarp all the layers are transformed into stone cells showing numerous pit canals (Figs. 113, 114). There is, however, a gradual merging of the lower and upper portions of the pericarp.

At maturity the fruit possesses a hard beak and the seeds are small and rounded with brown reticulate foldings on the surface. The seed consists of degenerated remnants of the integument, massive fatty endosperm and a large embryo. In this connection it may be added that the acanthaceous seeds are generally considered to be exalbuminous.

Systematic Position

In his monograph on the Acanthaceae, Lindau (1895) proposed four sub-families and except for minor changes this classification has generally been accepted. However, Bhaduri (1944) doubted the validity of the sub-family Nelsonioideae. Recently Bremekamp (1953) suggested that as originally constituted the family is not a natural assemblage and he splits it into three families, designating them as Thunbergiaceae, Mendonciaceae and Acanthaceae, synonymous with the sub-families Thunbergioideae, Mendoncioideae and Acanthoideae of Lindau. His main consideration for doing so is that there is not even a single character by which the members of the Acanthaceae can be distinguished from the members of the allied families.¹

Further, Bremekamp transferred the fourth sub-family Nelsonioideae to the sub-family Rhinanthoideae, tribe Rhinanthaeae, of the Scrophulariaceae. His main arguments are: "the presence of a well developed endosperm separates them from the true Acanthaceae and their nearest allies . . . , and suggests a place in the Scrophulariaceae. Most of the latter possess quite a different kind of placentation but in Rhinanthaeae we find a similar type, for here too the ovules are attached

¹ " . . . Lindau too did not succeed in finding a single character by which the family in its delimitation could be distinguished from its allies." (see Bremekamp, 1953).

in a double vertical row to the middle of the dissepiment, and also loculicidal capsules, opening the same way as in *Hiernia*, the dissepiment splitting along the axis and perpendicular to its surface."

How far the transfer suggested by Bremekamp is valid, can be judged from the following comparative table:

Character	<i>Elytraria</i> (Nelsonioideae)	Acanthaceae	Rhinantheae (Scrophulariaceae)
Habit	Rosette herbs with alternate leaves	Erect herbs or shrubs with opposite leaves	Semi-parasites with alternate or opposite leaves
Inflorescence	Scapigerous, racemose	Cymose	Cymose
Placentation	Parietal	Axile	Axile
Pollen grains	3-colporate (syncolpate), shed at the 2-celled stage	2 to 6 colpate, shed at the 2 to 3-celled stage	2 to 7 colpate (syncolpate), shed at the 2-celled stage
Ovule	Unitegmatic, tenuinucellate, amphitropous with a funicular obturator and a jaculator; integumentary tapetum present	Unitegmatic, tenuinucellate, anatropous with a jaculator; funicular obturator and integumentary tapetum absent	Unitegmatic, tenuinucellate, amphitropous; integumentary tapetum present
Embryo sac	Polygonum type; antipodal cells persistent, often become binucleate	Polygonum type; antipodal cells usually ephemeral	Polygonum type; antipodal cells ephemeral
Endosperm	Cellular, conforms to the Pedicularis type of Cr��t�� (1951); micropylar haustorium well developed; central chamber grows asymmetrically and lacks the free nuclear phase	Cellular; micropylar and chalazal haustoria present; central chamber grows asymmetrically and has a free nuclear phase	Cellular, conforms to the Pedicularis type; micropylar and chalazal haustoria well developed; central chamber grows symmetrically and lacks the free nuclear phase
Embryo	Conforms to Lythrum-variation of Onagrad type	Conforms to Lythrum-variation of Onagrad type	Conforms to Pedicularis-variation of Onagrad type
Seed	Albuminous, endosperm ruminant; testa absent	Exalbuminous; testa well developed	Albuminous; testa well developed
Fruit	Thick-walled, capsule with explosive dehiscence	Thick-walled, loculicidal capsule; explosive dehiscence	Thick-walled, loculicidal capsule

It is obvious from the above table that the Acanthaceae and Rhinanthaceae resemble each other in several embryological features like the occurrence of unitegmatic, tenuinucellate ovules; Polygonum type of em-

bryo sac and Cellular endosperm with chalazal and micropylar haustoria. *Elytraria* and Rhinanthaeae are also similar in some respects, e.g. the early segmentation of the endosperm in both correspond to the Pedicularis type (Crété, 1951). However, in its later growth the two differ fundamentally since the central endosperm chamber in the Rhinanthaeae grows symmetrically (Schmid, 1906; Krishna Iyenger, 1942; Crété, 1951; Berg, 1954) while in *Elytraria* it is prominently asymmetrical. This feature is shared with the rest of the Acanthaceae and is not known in the allied families (Mauritzon, 1934). Moreover, a jaculator is present in *Elytraria* and most other Acanthaceae, but is absent in the Rhinanthaeae.

Bremekamp (1953) has described the Acanthaceae as “familia *Tubiflorarum Thunbergiaceis, Mendonciaceis, Bignoniaceis, Pedaliaceis* affinis sed ovulis utroque loculo duobus superpositis vel pluribus ad medium septum in series verticales 2 vel rarissime 4 dispositis, capsula loculicida elastice dehiscente, septo eodem tempore in partes duas ad valvas adherentes fisso, seminibus appianatis retinaculis suffultis, ab eis distinguenda. Syn. *Acanthaceae* subfam. *Acanthoideae* Lindau”.² The seeds are said to be flat but in *Andrographis* (Acanthaceae) they are round (Mauritzon, 1934), as is also the case in *Elytraria*. In other features too *Elytraria* corresponds to the description of Acanthaceae by Bremekamp (1953). *Elytraria* differs from other members of the Acanthaceae in having alternate leaves, parietal placentation, integumentary tapetum, funicular obturator and albuminous seeds. In contrast, most of the Acanthaceae possess opposite leaves, axile placentation and exalbuminous seeds. The integumentary tapetum and funicular obturator are absent.

Thus, there is no doubt that the morphology and embryology of *Elytraria* is in general conformity with other members of the Acanthaceae, but there are also important dissimilarities. However, they do not warrant the transfer of *Elytraria* to the Scrophulariaceae, and, for the present, its inclusion in the family Acanthaceae, subfamily Nelsonioideae, appears to be the most satisfactory course.

² A family allied to the Thunbergiaceae of the Tubiflorae, Mendonciaceae, Bignoniaceae, Pedaliaceae, from which it is to be distinguished by two superposed ovules in each loculus, or by many ovules arranged near the median septum in two or very rarely in four vertical rows, by the loculicidal capsule dehiscing elastically, by the septum splitting at the same time into two parts which adhere to the valves, and by the seeds which are flattened and supported by retinacula. Syn. *Acanthaceae*, subfam. *Acanthoideae* Lindau.

Summary

In *Elytraria acaulis* the pentamerous flowers show two fertile stamens, three staminodes and 16—20 ovules borne on parietal placentae.

The anther wall comprises the epidermis, an endothecium which for the most part lacks fibrous thickenings, a single middle layer and the glandular tapetum.

The reduction divisions are simultaneous, cytokinesis occurs by furrowing and the tetrads are tetrahedral or decussate.

The microspores show three conspicuous longitudinal furrows which later on disappear due to enlargement of the pollen grain. The latter are shed at the two-celled stage.

The ovules are amphitropous, unitegmie and tenuinucellate. The inner epidermis of the integument gives rise to an integumentary tapetum as early as the megaspore tetrad stage. A weakly developed obturator and a jaculator differentiate from the funiculus.

The development of the embryo sac is of the Polygonum type. Usually both the synergids degenerate but one of them may become hypertrophied. The antipodal cells are persistent and often show a binucleate condition; occasionally four antipodal cells are seen.

Double fertilization has been observed and the remnants of the pollen tube persist during maturation of the seed.

The endosperm is of the Cellular type and the first division of the primary endosperm nucleus results in the formation of the chalazal haustorium and an upper cell. The latter divides to form the micropylar haustorium and the central chamber.

The micropylar haustorium shows one to five nuclei and is aggressive; the chalazal haustorium is two to four-nucleate and degenerates early. The central chamber is cellular from the very beginning, shows asymmetrical growth and forms the bulk of the endosperm.

The first division of the zygote is transverse and the development of the embryo corresponds to the *Lythrum*-variation of the *Onagrad* type.

The seed contains a ruminant fatty endosperm and a typical dicotyledonous embryo. Due to the aggressive activity of the endosperm, the integument is almost completely absorbed and the seed is practically without any testa.

The ovary wall comprises four to six layers of thin-walled parenchymatous cells but at maturity the epidermal cells of the pericarp and those adjacent to the inner epidermis become highly sclerified.

The genus *Elytraria* shows several morphological and embryological features which are not in common with the rest of the *Acanthaceae*, but there seems to be no justification for transferring it to the *Scrophulariaceae*.

We are indebted to Professor P. Maheshwari for advice; to Professors R. Souèges (Paris), V. Puri (Meerut) and V. S. Rao (Bombay) for comments concerning embryogeny and floral anatomy; to Professor C. E. B. Bremekamp (Utrecht) for supplying some of his publications on the delimitation of the family *Acanthaceae*; and to Rev. Father H. Santapau (Bombay) for translating some passages from Latin to English.

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Litteratur

FRIEDRICH BOAS: Zeigerpflanzen. 240 sid., 167 färgplanscher, 73 teckningar. Verlagsgesellschaft für Ackerbau mbH., Hannover 1958. DM 26.—.

När det gäller att bedöma en odlingsmark brukar vi här i Sverige nästan uteslutande tillämpa geologisk-genetiska och kemisk-fysikaliska synpunkter. Att detta inte är det enda sättet att kunna komma till en uppfattning om en jords beskaffenhet, visar en rad utländska forskningar på ogräsekologins och sociologins område. Enligt dessa forskningar lämnar ett flertal vanliga åkerogräs pålitliga uppgifter om en jords struktur, lerandel, näringsämneshalt (främst kväve), vatten- och temperaturförhållanden, surhetsgrad (kalkhalt) osv. Man kan utnyttja dem som ekologisk-biologiska värdemätare. De kan ge en fingervisning, vilka kulturåtgärder som kan vara lämpliga.

Det rubr. verket kan betecknas som en sammanfattning av och ett försök till samordning av nämnda spridda forskningar, varvid huvudvikten lagts vid den praktiska tillämpningen av vunna erfarenheter, bland vilka författarens egna utgör en väsentlig del.

Det bör framhållas, att endast tyska förhållanden behandlas, och att rönen givetvis inte utan inhemska undersökningar kan tillämpas för vårt åkerbruk. Men att en biologisk syn på jordfrågorna kan innebära en värdefull komplettering till den fysikalisk-kemiska synen, att vidare ett sådant betraktelsesätt kan vara ett inspirerande och roande moment för en lantbrukare och botaniskt intresserad är alldeles uppenbart. Man hälsar därför en framställning som föreliggande med glädje och frågar efter en motsvarighet på svenska. Den finns tyvärr inte, vilket emellertid inte innebär, att forskningen i Sverige varit blind för ifrågavarande spörsmål, men utredningarna har inte avancerat så långt ännu, att de kan utgöra en grundval för en jämförelse av förhållandena.

Färgplanschdelen — 167 st. förnämliga bilder — visar ogräsen i naturlig miljö. Man får i många fall även en presentation av en bestämd ogräsarts följeslagare i åkern. Bildtexten består av en kort karakterisering av de jordegenskaper arten kan ge upplysning om.

Här följer ett litet axplock ur textdelen för att ge en överblick över räckvidden hos lagbundenheterna i vegetationens sammansättning på bestämda ståndorter.

Chrysanthemum segetum (gullkrage) indikerar, där den förekommer i stationära och växtliga bestånd, relativt hög markfuktighet i kemiskt sura, sandiga lerjordar (låga pH-värden). Växtgeografiskt är den karakteriserad som västlig.

Riklig förekomst av *Scleranthus annuus* (grönknavel) tyder i sällskap med *Rumex acetosella* (bergsyra) på sura och näringsfattiga förhållanden och grund sandjord. Höjning av kvävehalt kan slå ut *Scleranthus* på sådana marker. I sällskap med bl.a. åkerrättika (*Raphanus raphanistrum*) och spergel (*Spergula arvensis*) koloniserar *Scleranthus* även bättre sand. Finns den på lerhaltig jord, så är sandandelen alltid hög. *Papaver rhoeas* (kornvallmo) förekommer däremot aldrig på kalkfattiga marker och skvallrar om lerhalt. Tillsammans med åkersenap pekar den dessutom på lerjord med ett mer eller mindre gynnsamt humustillstånd. *Papaver rhoeas* och *Scleranthus annuus* betecknas som ståndortsantipoder, dvs. arter som utesluter varandra. Detta gäller även för åkersenap och åkerrättika. Den senare är hemma i kalkfattig miljö.

Även den besvärliga våtarven (*Stellaria media*) har sitt indikatorvärde: den når sin bästa utveckling i jord med aggregatstruktur och god kväveförsörjning. Övriga kvävevisare är *Solanum nigrum* (nattskatta), *Galium aparine* (snärjmåra), *Senecio vulgaris* (korsört), i andra hand åkersenap, åkerrättika och *Thlaspi arvense* (penningört). På högvärdiga, lättbrukade, svagt leriga sandjordar med god genomluftning utan stagnerande fuktighet under någon längre tid och med (nästan) veteduglighet pekar *Arabidopsis thaliana* (backtrav), *Papaver argemone* (spikvallmo) och *Fumaria officinalis* (jordrök), medan åkersenap även är utbredd på styv lera. Som en känslig och pålitlig indikator på till och med små mängder ler uppges *Sherardia arvensis* (blåmadra), som tillsammans med *Euphorbia exigua*, åkersenap och åkerrättika är typiska för lättlera.

Markfel och bruksningsfel förråder *Gnaphalium uliginosum* (sumpnoppa), *Plantago major* (groblad), *Plantago intermedia* och *Mentha arvensis* (åkermynta), ibland även *Apera spica-venti* (åkervan, kösa), där det rör sig om igen-smetade eller igenslammade ställen. Åkertisteln (*Cirsium arvense*) trivs bäst på näringsrika, djupa lerjordar, säger dock inte mycket om pH-värdet, men undviker kalkfattiga sandmarker. Även vid lätt beskaffenhet av ytjorden återspeglar den lerlager längre ner. Flyghavrens (*Avena fatua*) utsaga är: styv till plastisk lera, cirkumneutral till alkalisk reaktion, låga värmeanspråk, aldrig stationär på lerbattig sand. *Tussilago farfara* (hästhov) inställer sig på kalkförande lera med rörligt grundvatten eller på kalkgrus, skred- och råmarkställen.

För en svensk läsare (även den botaniskt skolade) innebär de tyska växtnamnen, som dominerar i texten, en viss svårighet, man tvingas slå mycket i innehållsförteckningen och bilddelen, för att klara nomenklaturen. Rubrik-sättningen kunde kanske vara något överskådligare. Till verkets starka sidor hör att även lekmannen tack vare färgbilderna, ritningarna och den lättförståeliga behandlingen av ämnet kommer till rätta med problemen. För fackmannen innebär mängden av nya vyer, ekologiska och sociologiska data en utvidgning av kunskapsstoffet på denna sektor och många tankeställare.

Pedagogiskt skickliga bildförklaringar avrundar intrycket av att boken fyller sin uppgift på ett föredömligt sätt. För intressets skull kan nämnas att färgdiapositiv kan erhållas av färgbildserien.

H. MERKER

Modern Developments in Plant Physiology. Report of seminar held August 26th to 30th, 1957. — Edited by P. MAHESHWARI. — Botany Department, University of Delhi, Delhi, India. 1957. 170 sider.

Dette er en samling av foredrag som ble holdt ved Universitetet i Delhi i forbindelse med at Dr. Kenneth V. Thimann, Harvard University, USA besøkte India. Dr. Thimann gir en god karakteristikk av samlingen i et forord der han uttrykker: ». . . More than a seminar in the American sense, this week-long conference was really an All-India Congress on Plant Physiology . . .» Vi kan godt skrive under på dette. Seminaret, eller la oss kalle det kongressen, var inndelt i seks seksjoner. A: Growth and Metabolism; B: Photoperiodism, Vernalization and Growth Regulating Substances; C: Organ and Tissue Culture; D: Physiology of Pollen; E: General Physiology; F: Physiology of Fungi. Det er tilsammen 52 artikler, en oversiktsartikkel, resten originalarbeider.

En stor del av den plantefysiologiske forskning i India angår vekst og vekst-regulerende substanser og objektene er for en stor del, naturlig nok, valgt blandt nyttevekstene. Men også metabolismen er viet temmelig stor oppmerksomhet. Eksempelvis ble det framlagt resultater fra undersøkelser over acetaldehyds virkning på respirasjonen i grønne blad, og over proteinnedbrytningen i avkuttete blad. — I seksjonen over organ- og vevkulturer er det hele ti artikler.

Indisk vitenskap er i rask utvikling. Denne boken gir et nyttig, og vi må formode representativt, tverrsnitt av noen av indiske plantefysiologers arbeidsområder.

PER HALLDAL

Notiser

Ny professor. Till professor i botanik, särskilt fysiologi, vid Stockholms högskola har från den 1 juli 1959 utnämnts fil. dr N. E. T. Hemberg.

Docentförordnande. Till docent i skogsbotanik vid Skogshögskolan har förordnats fil. dr E. Uggla.

Utmärkelser. F. akademiträdgårdsmästare Axel Törje promoverades den 30 maj 1959 till fil. hedersdoktor vid Lunds universitet. Fil. dr H. Lamprecht, Landskrona, har tilldelats professors namn.

Doktorsdisputationer. Tekn. lic. Börje Wickberg disputerade den 20 april 1959 i Stockholm på en avhandling: »Studies on algal chemistry». Vid Uppsala universitet försvarade fil. lic. Göran Stenlid den 13 maj avhandlingen: »Studies on the inhibitory effects of sugar upon plant roots». Fil. lic. Brita Lundblad ventilerade den 19 maj vid Stockholms högskola arbetet: »Rhaeto-liassic floras and their bearing on the stratigraphy of Triassic-Jurassic rocks». Vid Lunds universitet försvarade slutligen fil. lic. Arne Gustavsson den 22 maj gradualavhandlingen »Studies on Nordic Peronosporas».

Forskningsanslag. K. Vetenskapsakademien har i februari 1959 utdelat följande stipendier för botaniska undersökningar: Till lektor E. Almquist 1.700 kr. från Harald E. Johanssons minnesfond för hieraciologiska studier i Uppland; till docent B. Pettersson 750 kr. ur K. O. E. Stenströms fond för växtbiologiska undersökningar; till f. assistent C. G. Alm 700 kr. ur Krokska fonden för botaniska undersökningar i norra Norrbotten och till docent M. Wærn 700 kr. ur samma fond för studier av algvegetationen på skalbottnar i Bohuslän.

Fysiografiska sällskapet i Lund har i mars 1959 utdelat bl.a. följande anslag: Till fil. kand. Folke Andersson och fil. mag. Jan Ericson 1.500 kr. för undersökning av fuktighetsförhållandena i skånska hed- och ängssamhällen; till fil. kand. Hugo Andersson 2.900 kr. för undersökningar över orsakerna till vissa korn-typers resistens mot angrepp av vanliga fritflugan; till docent Hellmuth Hertz 860 kr. för undersökning av den geoelektriska effekten hos växter; till amanuens H. Merker 1.000 kr. för markundersökningar i samband med en inventering av ogräsfloran inom området mellan Lund och Landskrona; till docent Hans Runemark 400 kr. för upprättande av ett hålkortsregister över systematisk och floristisk litteratur över medelhavsområdet; till sektionen Skånes Flora 800 kr. för fältundersökningar över Skånes

flöra under 1959. Ur Nilsson-Ehle-fonden utdelades 935 kr. till fil. dr Nils O. Bosemark för undersökning över accessoriska kromosomer hos *Phleum phleoides*; till fil. kand. Gunnar Ising 1.800 kr. för studier över pollenfertilitet hos ett antal F₁-kombinationer av olika kornsorter; till professor Arne Muntzing 1.500 kr. för vissa vid Lunds genetiska institution bedrivna undersökningar; till docent Nils Nybom 1.900 kr. för polyploidiseringsarbeten inom *Pomoideae* samt 2.600 kr. för cytogenetiska studier inom *Rubus*; dessutom har i en del fall anslag beviljats för fortsättning av tidigare påbörjade undersökningar.

Längmanska kulturfonden har våren 1959 utdelat bl.a. följande anslag: till fil. lic. Rolf Dahlgren, Lund, 2.000 kr. för illustrationer, kartor och diagram i en avhandling med titeln »Revision of the *Aspalathus* species with flat leaflets»; till laborator B. Kullenberg, Uppsala, 3.000 kr. för vissa kostnader för en avhandling med titeln »Studies in *Ophrys* pollination»; till docent B. Pettersson, Uppsala, 2.000 kr. för fortsatta undersökningar rörande dynamik och konstans i Gotlands flora och vegetation samt förarbeten till ett arbete om Gotska Sandöns flora och vegetation.

Statens naturvetenskapliga forskningsråd har vid sammanträde den 20 mars 1959 utdelat bl.a. ett anslag å 11.640 kr. till professor R. Florin, Stockholm, för undersökningar beträffande 1) morfologi, anatomi och systematik hos barrträd (prof. R. Florin och fil. mag. J. Tengnér), 2) systematisk embryologi hos *Compositae* (docent G. Harling); vidare ett anslag å 3.969 kr. till docenterna B. Lökvist och H. Runemark, Lund, för kromosomtalsbestämning av skånska växter samt material från Cykladerna, samt ett anslag å 6.000 kr. till professor Fredrik Nilsson, Alnarp, för cytogenetiska studier inom släktet *Ribes*.

Ur Wilhelm och Martina Lundgrens vetenskapsfond har d. 20 april till professor Bertil Lindquist, Göteborg, utdelats ett anslag på 10.000 kr. för botaniska studier i Amerika och Japan.

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Tables should be written on separate sheets and accompanied by explanatory headings. Figure legends and references should be written on separate sheets. Figures should be numbered with Arabic numerals. If in several parts, the single parts should be indicated by letters. Foot-notes should be avoided.

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